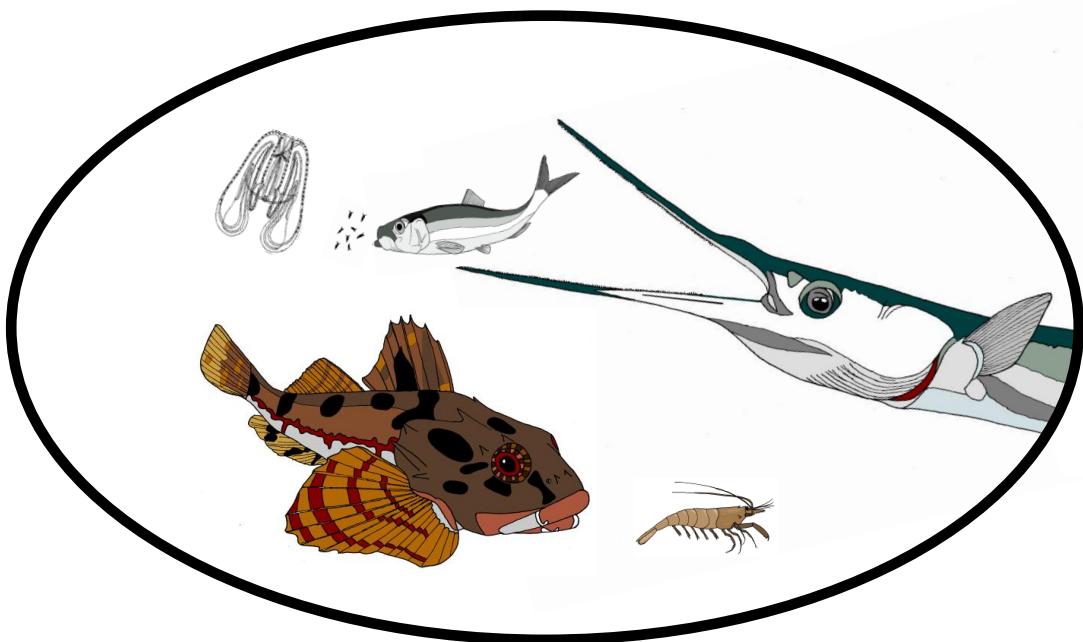


# The trophic structure of a Wadden Sea fish community and its feeding interactions with alien species

Die trophische Struktur einer Fischgemeinschaft des Wattenmeeres und deren Fraßinteraktionen mit gebietsfremden Arten



## DISSERTATION

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**Florian Kellnreitner**

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Referent: Dr. habil. Harald Asmus

Korreferent: Prof. Dr. Thorsten Reusch

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## Summary

The Wadden Sea is an important nursery area for commercial fish species of the North Sea and habitat for many small fish species. It is a very variable habitat with high variations in salinity and temperature. The Wadden Sea ecosystem has been modified by the utilization of humans since millineries. Species composition and food web of the fish of the Wadden Sea are influenced by destruction and alterations of habitats, fisheries, introduced species and climate change.

The species distribution shows marked differences in species occurrence between inter- and subtidal areas and between the 4 different seasons of a year. *Pomatoschistus microps* was the most abundant fish species in intertidal areas and *Clupea harengus* and *Ammodytes tobianus* were abundant in subtidal areas. Variation was also discovered in the occurrence of feeding guilds found by diet overlap calculations. Only calanoid copepod eaters and *Crangon crangon* eaters were present year round. Fish of the Sylt-Rømø Bight show a broad spectrum of prey and opportunistic feeding behavior. Convergence towards abundant prey organisms in summer and divergence of feeding in winter was observed. An increase in the abundance of zooplanktivorous fish compared to previous investigations was found.

Stable isotope analysis of carbon and nitrogen revealed a lower mean trophic position for zooplanktivorous fish than for fish feeding on zoobenthos. *Merlangius merlangus* was found at the highest trophic position (3.84) and *Limanda limanda* at the lowest (2.94). The overall low trophic position of the fish of the Sylt-Rømø Bight pointed to short food chains and therefore to an immature ecological state of the bight.

Immature systems are characterized by a high degree of unutilized resources and are therefore more susceptible to introductions of new species. The influence of these species on native fish was shown in the example of the herring (*Clupea harengus*) and 2 new species in the food web, the sea walnut (*Mnemiopsis leidyi*) and the sand smelt (*Atherina presbyter*).

The sea walnut was introduced into the North Sea most likely between the year 2000 and 2006. It first occurred in samples in early summer and reached its highest abundance in fall ( $10.3 \pm 8.2$  individuals  $m^{-3}$ ). Herring and sea walnut showed temporarily high diet overlap which was related to the high amount of ingested calanoid copepods by both species. High amounts of bivalve larvae were found in the diet of the sea walnut in August, which could not be found in the guts of herring. In an experiment it was

demonstrated that in herring intraspecific competition was significantly higher than competition from the sea walnut. Nevertheless, competition between both species could occur if their feeding resources should be limited.

The distributional range of the sand smelt was possibly extended to the North due to increasing sea water temperatures induced by climate change. Only recently increasing abundance of this fish species in the Sylt-Rømø Bight is observed. The results of our investigation show only a temporarily high diet overlap due to ingestion of nauplius and cypris larvae of both species. The sand smelt shows positive selection of these meroplankton and avoidance of calanoid copepods, which are the main diet of herring.

There is still place for new species in the food web of the Sylt-Rømø Bight. Its biology determines how a new species will integrate into the food web. The sea walnut poses a potential threat to native zooplanktivores due to overlapping diets and its high fertility and abundance. This potential increases should the competition pressure from native fish be reduced. The sand smelt uses mainly different habitats than native zooplanktivorous fish and could therefore integrate into the fish food web.



## Zusammenfassung

Das Wattenmeer ist ein wichtiges Aufwuchsgebiet vieler kommerzieller Fischarten der Nordsee und Lebensraum für viele kleinbleibende Fischarten. Es stellt einen sehr variablen Lebensraum dar der sich durch große Salinitäts und Temperaturunterschiede auszeichnet. Das Wattenmeer ist seit Jahrtausenden durch die Nutzung des Menschen geprägt. Zerstörung und Veränderung von Habitaten, Fischerei, eingeschleppte Arten und Klimawandel üben Einflüsse auf Artenzusammensetzung und Nahrungsnetz der Fische des Wattenmeeres.

Die Untersuchung der Artenverteilung der Fische der Sylt-Rømø Bucht zeigt deutliche Unterschiede zwischen inter- und subtidalen Bereichen und innerhalb dieser zwischen den verschiedenen Jahreszeiten. Über das gesamte Jahr gemittelt sind *Pomatoschistus microps* in den intertidalen und *Clupea harengus* und *Ammodytes tobianus* in den subtidalen Bereichen am häufigsten. Auch die durch Berechnung von Nahrungsüberlappungen gefundenen Nahrungsgilden variieren stark zwischen den Jahreszeiten. Nur calanoide Kopepoden Fresser und *Crangon crangon* Fresser waren das ganze Jahr hindurch vorhanden. Die Fische der Sylt-Rømø Bucht zeigten generell ein breites Beutespektrum und opportunistisches Fressverhalten. Es wurde eine Konvergenz zu häufigen Beuteorganismen im Sommer und einer Divergenz im Fressverhalten im Winter beobachtet. Ein Anstieg in der Anzahl zooplanktivorer Fische im Vergleich zu vorangegangenen Untersuchungen konnte gezeigt werden.

Die Analyse der Isotopenzusammensetzung von Kohlenstoff und Stickstoff zeigte eine durchschnittlich niedrigere trophische Position für zooplanktivore Fische als für benthivore Fische. Die höchste trophische Position wurde für *Merlangius merlangus* gefunden (3,84), die niedrigste für *Limanda limanda* (2,94). Die generell niedrige trophische Position der Fische der Sylt-Rømø Bucht deutet auf kurze Nahrungsketten und somit auf ein unreifes ökologisches Stadium der Bucht hin.

Unreife Systeme zeichnen sich durch ein hohes Maß an ungenutzten Ressourcen aus und sind somit anfälliger für eingeschleppte Arten. Der Einfluss dieser Arten auf die heimische Fischfauna sollte anhand des Herings (*Clupea harengus*) und zweier neuer Arten im Nahrungsnetz, der Meerwalnuss (*Mnemiopsis leidyi*) und des Ährenfisches (*Atherina presbyter*) gezeigt werden.

Die Meerwalnuss wurde vermutlich kurz nach der Jahrtausendwende in die Nordsee eingeschleppt. Sie war ab Juni in den Planktonproben und erreichte ihre größte Dichte

im Herbst ( $10.3 \pm 8.2$  individuals  $m^{-3}$ ). Hering und Meerwalnuss zeigten eine zeitweise hohe Nahrungsüberlappung die auf die starke Nutzung beider Arten von calanoiden Kopepoden zurückzuführen war. Die Meerwalnuss zeigte im August eine starke Nutzung von Bivalvialarven die beim Hering nicht zu finden war. Durch ein Experiment wurde gezeigt, dass beim Hering die intraspezifische Konkurrenz significant höher ist als die Konkurrenz durch die Meerwalnuss. Konkurrenz zwischen diesen beiden Arten könnte jedoch auftreten sollten die Nahrungsressourcen limitiert sein.

Der Ährenfisch hat sein Verbreitungsgebiet vermutlich durch den Klimawandel und den damit verbundenen Temperaturanstieg in den Norden erweitert. Im Bereich der Sylt-Rømø Bucht wird diese Fischart erst seit kurzem in hohen Dichten beobachtet. Die Ergebnisse unserer Untersuchungen zeigen eine teilweise hohe Nahrungsüberlappung, die hier allerdings auf Nauplien- oder Cypris-Stadien von Crustaceen zurückzuführen ist. Der Ährenfisch zeigte positive Selektion von diesen Meroplanktonarten und Vermeidung von calanoiden Kopepoden, die meist den Hauptbestandteil der Nahrung des Herings ausmachen.

Zusammenfassend kann davon ausgegangen werden, dass noch Platz für neue Arten im Nahrungsnetz vorhanden sind. Wie sich eine neue Art in das Nahrungsnetz eingliedert hängt von ihrer Biologie ab. Die Meerwalnuss kann durch ihre hohe Reproduktionsfähigkeit potentiell eine Gefahr für die Zooplankton Frassgilde darstellen, vor allem wenn der Konkurrenzdruck durch heimische Fische wegfallen sollte. Der Ährenfisch nutzt hauptsächlich andere Habitate als die heimischen zooplanktivoren Fische und könnte sich somit ins Nahrungsnetz integrieren.

## 1. General Introduction

### 1.1. The fish of the Wadden Sea

The Wadden Sea plays an important role as habitat for small sized fish species and as nursery area for many commercial fish species (Rauck and Zijlstra 1978). It is characterized by a high production supplying juvenile fish with food and the turbid waters provide some protection from predation (Blaber and Blaber 1980). Nevertheless, the Wadden Sea is a dynamic system and organisms living there require a high amount of flexibility to adapt to fluctuating environmental parameters such as high variations of temperature and salinity. The variations of these abiotic but also biotic factors such as food resources lead to changing fish abundance and distribution within the tidal rhythm and the different seasons of a year (Herrmann et al. 1998).

Important factors influencing species composition are the connection of the particular Wadden Sea area to both, the North Sea and rivers as well as other fresh water discharges. Sediment composition and depth profile are additional parameters that structure the fish community (Herrmann et al. 1998, Hinz 1989, Vorberg and Breckling 1999). As the study area of this thesis is the Sylt-Rømø bight the following information refer mostly to the northern part of the Wadden Sea.

Seasonal changes, as mentioned above, have a strong impact on the abundance and the distribution of the fish species in the Wadden Sea (Herrmann et al. 1998, Jansen 2002). Fish use the Wadden Sea for multiple reasons to which their occurrence is related. The 63 fish species listed in Vorberg and Breckling (1999) were never encountered in the same season and some not even in the same year. Few species occur in the Wadden Sea the whole year round (Vorberg and Breckling 1999) and during their whole life cycle. Among them are the hook nose (*Agonus cataphractus*), the common goby (*Pomatoschistus microps*) and the eel pout (*Zoarces viviparus*). The hook nose and the eel pout are boreal species with a northern distribution. They tolerate low temperatures in winter and are only affected by exceptionally high temperatures in summer (Pörtner and Knust 2007). The common goby is a Lusitanian species with a southern distribution. It migrates to deeper and warmer areas within the Wadden Sea in winter.

Other species are present nearly year round but regularly leave the Wadden Sea. Examples are the sand goby (*Pomatoschistus minutus*) and the lesser pipefish

(*Syngnathus rostellatus*) which migrate into the adjacent North Sea and the flounder (*Platichthys flesus*) which also migrates into estuaries and rivers (Kerstan 1991).

Fish species use the area for feeding, as nursery or spawning grounds (Vorberg and Breckling 1999). Herring (*Clupea harengus*), plaice (*Pleuronectes platessa*), sole (*Solea solea*) and sprat (*Sprattus sprattus*) use the Wadden Sea as nursery habitat (Vorberg and Breckling 1999). The garpike (*Belone belone*) enters the Wadden Sea in spring for spawning (Polte et al. 2006, Rosenthal and Fonds 1973). The lesser sand eel (*Ammodytes tobianus*) and the Atlantic makerel (*Scomber scombrus*) are present in summer in large swarms to feed. Anadromous fish such as the smelt (*Osmerus eperlanus*) spawn in fresh water and migrate through the Wadden Sea area in the cold season (Anders and Wiese 1993). Catadromous fish such as the eel (*Anguilla anguilla*) and the flounder (*Platichthys flesus*) spawn outside the area in the North Sea or the Atlantic ocean but enter the Wadden Sea as juveniles and partly ascend further to estuaries and rivers.

The rhythm of the tides influences distribution of fish species on a daily basis. Fish migrate into intertidal areas for reproduction, avoidance of predation and feeding (Gibson 1993). The garpike spawns in the intertidal seagrass beds in spring (Polte and Asmus 2006). The common goby is a typical species which migrates on tidal flats for feeding (Hampel and Cattrijsse 2004, Kellnreitner 2007). Juvenile individuals remain in tidal pools or intertidal seagrass beds during low water, most likely to avoid predators (Polte et al. 2005).

Apart from natural factors human activities have strongly affected fish species abundance, distribution and composition (Lotze 2005, 2007). Demersal fish were important fishery resources for people living in the Wadden Sea region since the 1<sup>st</sup> century AD (Enghoff 2000, Lotze 2005, Lozan 1994). Nowadays large demersal fish are rare in the Wadden Sea area and rays have completely disappeared as a result from overexploitation (Wolff 2000).

Also diadromous fish were an important fishery resource since Roman times (Prummel and Heinrich 2005). In addition to fishery diadromous fish were also heavily affected by riverine pollution and habitat degradation through damming of rivers and destruction of spawning grounds (Hoffmann 2005, Lotze 2005). Today allis shad (*Alosa alosa*), houting (*Coregonus oxyrinchus*), salmon (*Salmo salar*) and sturgeon (*Acipenser sturio*) are either extinct or critically endangered in the Wadden Sea (Fricke et al. 1995).

Fish species using *Zostera marina* sea grass beds as habitat or spawning ground were affected by the “wasting disease” which destroyed these sea grass meadows in the 1930s (Giesen et al. 1990). Greater pipefish (*Syngnathus acus*), snake pipefish (*Entelurus aequoreus*), deep-snouted pipefish (*Syngnathus typhle*) and sea stickleback (*Spinachia spinachia*) are today vulnerable or endangered (Fricke et al. 1995) and the herring lost important spawning grounds (Wohlenberg 1935).

## 1.2. Fish feeding ecology and the fish food web of the Sylt-Rømø bight

Gerking (1994) defines fish feeding ecology “...as what organisms are fed upon, or food habits, how fish acquire their food, or foraging habits and to a lesser extent where fish forage, or the foraging habitat.” A basic principle of fish feeding ecology (and feeding ecology in general) is the notion of trophic levels. The conceptual scheme was developed by Lindeman (1942). The trophic level represents the position organisms occupy in the food chain. Autotrophic organisms are at the base of the food web, at trophic level 1. Consumers of autotrophs are at trophic level 2, predators at trophic level 3 and the top predators occupy a trophic level of 4 or higher. However, a certain organism feeds in most cases on different trophic levels and the use of discrete trophic levels therefore fails to describe the complex feeding interactions in marine environments adequately (Post 2002). Today the use of new methods and models allows estimation and even measurement of continuous trophic positions that lead to deeper insights into energy or mass flow through the often complex marine food webs (Peterson and Fry 1987, Post 2002).

One of the first scientists working on feeding of fish on an ecosystem wide level was Forbes (1878, 1883). The analysis of stomach or gut contents was the only method to gain insights into fish nutrition in the beginning of scientific work on fish feeding ecology (Hyslop 1980). Depending on the species analyzed and research questions several indices based on prey number, volume, occurrence, weight and also subjective estimates of the contribution of a food type to the diet were applied (reviews by Hynes 1950 and Hyslop 1980). A constraint of working only with stomach and gut analyses is a high variation caused by individual feeding habits, food availability, differential digestibility of prey, seasonality and other factors (Pinnegar and Polunin 1999, Polis and Strong 1996). Stable isotope analysis as a method to resolve some of these constraints was developed in the end of the last century (De Niro and Epstein 1978, Minagawa and Wada 1984). It is based upon the principle that everywhere on earth elements are present in lighter and heavier atomic weights. These variants of the same element are

called isotopes. The ratio of heavy to light isotopes in the environment is depending on the element and can vary from region to region. It is either reflected or altered in the tissue of the autotrophic organisms and the following trophic levels living in this environment and depending on these autotrophic sources (Peterson and Fry 1987). Heavy nitrogen isotopes are enriched for a certain amount at each trophic transfer and trophic position can be calculated (Minagawa and Wada 1984). While stomach analysis represent a relatively short time scale in terms of digestion time, stable isotope respond to longer time periods of physiological processes such as tissue turnover. The combination of gut content and stable isotope analysis therefore offers deeper insights into the diet spectra of fish and their trophic position than ever before (Pasquaud et al. 2010)

Work on fish diets in the Wadden Sea considering the whole fish community is scarce. Most of the studies investigated single species, a selection of commercially important species (e.g. Daan 1973, Hamerlynck and Hostens 1993, Last 1987, Robb and Hislop 1980), did not consider different seasons (Hostens and Mees 1999) or were restricted to subtidal areas (Nawratil 2009). A lot of work on feeding relationships was done in the frame of an interdisciplinary program SWAP (Sylter Wattenmeer Austauschprozesse – Wadden Sea Sylt exchange processes). This work resulted in consumption estimates for some of the most important fish species at this time (Herrmann et al. 1998) and in the construction of a food web model for the bight (Asmus and Asmus 2000, Baird et al. 2004, Baird et al. 2007). In the food web of the Sylt-Rømø bight 7 of the most dominant fish species were represented (Fig. 1.1)

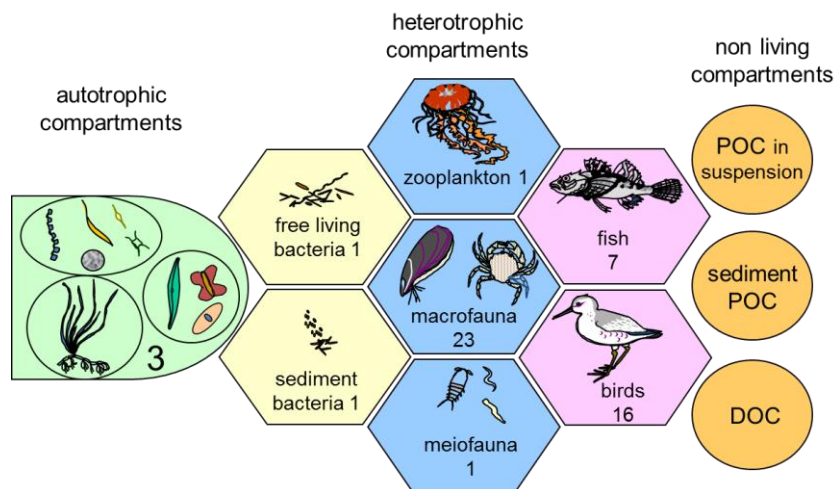


Fig. 1.1 Food web of the Sylt-Rømø bight (simplified after Baird et al. 2004). The food web comprises 59 compartments including 7 fish species.

Since the end of the SWAP-project the area of the Sylt-Rømø bight and the Wadden Sea in general underwent several profound ecosystem changes. The most evident change was the spread of the Pacific oyster (*Crassostrea gigas*) (Diederich, 2006, Nehls et al. 2006, Reise 1998). This species was introduced into the Wadden Sea for aquaculture purposes in 1986. Single individuals were observed on native mussel beds (*Mytilus edulis*) in the beginning of the 1990s and started to increase in the beginning of the 21 century. Today the pacific oyster covers almost all former mussel beds on the coast of Sylt (Diederich 2006, Nehls et al. 2006). Together with the also introduced razor clam *Ensis americanus* and slipper limpet *Crepidula fornicata*, they form a large filter feeding biomass that could influence the food web (Chauvaud et al. 2000, Nehls et al. 2006, Reise and van Beusekom 2008). Abundance of the barnacle *Austrominius modestus*, introduced in 1955 increases since the late 1990s and has recently surpassed abundances of native barnacles (Witte et al. 2010). Since 2006 the sea walnut *Mnemiopsis leidyi*, a voracious planktivorous ctenophore (Burrell and van Engel 1976) is observed in Wadden Sea (Boersma et al. 2007, Faasse and Bayha 2006). And these are only a few examples of more than 80 species that have been introduced into the North Sea and the adjacent Wadden Sea (Reise et al. 1998, Reise et al. 2005) a lot of them increasing in abundance in particularly the last decade (e.g. Buschbaum & Gutow 2005, Nehls et al. 2006, Witte et al. 2010). Also the appearance and the increase in abundance of these alien species was recorded by the above mentioned authors, only few quantitative attempts were made to understand the role of these species in the food web and to assess their ecological impact on system level (Baird et al. 2004; 2007; 2008).

### 1.3 Interaction of native species with alien species

Marine species non native to an area are either intentionally or unintentionally introduced by men (Alpert 2006) or have extended their native range due to climate change (Walther et al. 2002) or new passages between different habitats (e.g. Goren and Galil 2005). If an alien species establishes in a new environment and alters the functioning of the ecosystem or its structure by exerting detrimental effects on native species it becomes invasive (Lodge 1993, Williamson 1996). The detrimental effects on native species are either direct or indirect. Direct effects are exerted through predation, parasitism and interference of reproduction. Examples for indirect effects are exploitative competition, cascading trophic effects and alteration of habitats or ecosystem processes (Crossland 2000, Wootton 1994).

Until now work on the interaction of alien species with Wadden Sea or North Sea fish is scarce. A study by Polte and Buschbaum (2008) on the introduced sea weed *Sargassum muticum* showed that it possibly promotes re-colonization of the snake pipefish in the Wadden Sea area. One case of an introduced species parasitizing on native fish is described (Hartmann 1993). The nematode *Anguillicoloides* (former *Anguillicola*) *crassus* lives in the swim bladder of eels (*Anguilla anguilla*) and feeds on their blood. It was introduced with imports of living eels from Japan in the 1980s and causes mortalities in European eel populations (Kirk 2003). Also indirect effects are possible through changes at the base of the food web. Byrnes et al. (2007) stated that most of the introduced species in the Wadden Sea occupy low trophic levels, while extinct species were positioned in higher trophic levels. This signifies an increase of species with weak interactions and could entail consequences for the ecosystem stability (McCann et al. 1998) which would affect fish at higher trophic levels. Some of these species were introduced very recently (Boersma et al. 2007) or becoming increasingly common (Witte et al. 2010). Two of these species, the sea walnut (Fig. 1.2B) and the sand smelt (Fig. 1.2C) are in the focus of this thesis and will be described more detailed.

These two species are very different in their history of geographic extension. The sea walnut originates from the east coast of America and was first introduced into the Black Sea via ballast water in the 1980s (Shiganova 1998). From there it was introduced to the Caspian Sea in the 1990s and also spread to the Sea of Azov, Marmara and the Mediterranean (Purcell et al., 2001), where it has recently reached the coast of Spain (Fuentes et al. 2010). In a second introduction it was brought to the Baltic and North Sea where it was first observed in 2006 (Boersma et al. 2007, Reusch et al. 2010). The sea walnut is recognized as invasive species, which easily establishes in a new environment as it tolerates a wide range of temperature (4-32°C) and salinity (4-38‰) (Javidpour et al. 2006). It is very fertile and produces up to 6200 eggs per day. First maturity is reached at a size of 15 mm (Finenko et al. 2006). In the Black Sea the rise of the sea walnut coincided with a dramatic decline in fishery yield of pelagic fish species. It was discussed controversially if pelagic fish were outcompeted by the sea walnut or if overfishing was the primary cause (Bilio and Niermann 2004). Competition between fish and the sea walnut was proposed (Hamer et al. 2011, Javidpour et al. 2009) but never investigated. The sea walnut has been introduced into the North and Wadden Sea by human vectors and is therefore considered as alien or introduced species (Boersma et al. 2007).

The status of the sand smelt is not as easy to define. The distribution range is on the European Atlantic coast from the Canary Islands in the South up to the British Isles in the



North (Quignard and Pras 1986). The distribution reaches farther north on the western side of the British Isles (Kislalioglu and Gibson 1977) than on the North Sea side (Rogers et al. 1998). In the Wadden Sea it most likely spread naturally to the North along the coastline (Francisco et al. 2009). However, it is likely that this expansion is promoted by increasing warmer temperatures caused by, possibly human induced, global warming as shown for other species (Cheung et al. 2009, Rose 2005). The sand smelt is a fast growing, pelagic fish species and reaches first maturity after the first year of life at a size of approximately 70 mm (Moreno et al. 2005). The sand smelt shows opportunistic feeding behaviour with zooplankton, small benthic crustaceans and annelids as prey (Kislalioglu and Gibson 1977, Pombo et al. 2005).

It is hypothesized that most interactions between alien species and Wadden Sea fish are related either to changes in feeding interactions (predation, competition, cascading trophic effects) or to alterations of habitats (eg. Polte and Buschbaum 2008). This thesis is about the feeding interactions of Wadden Sea fish and will focus on competition with new species in this area.

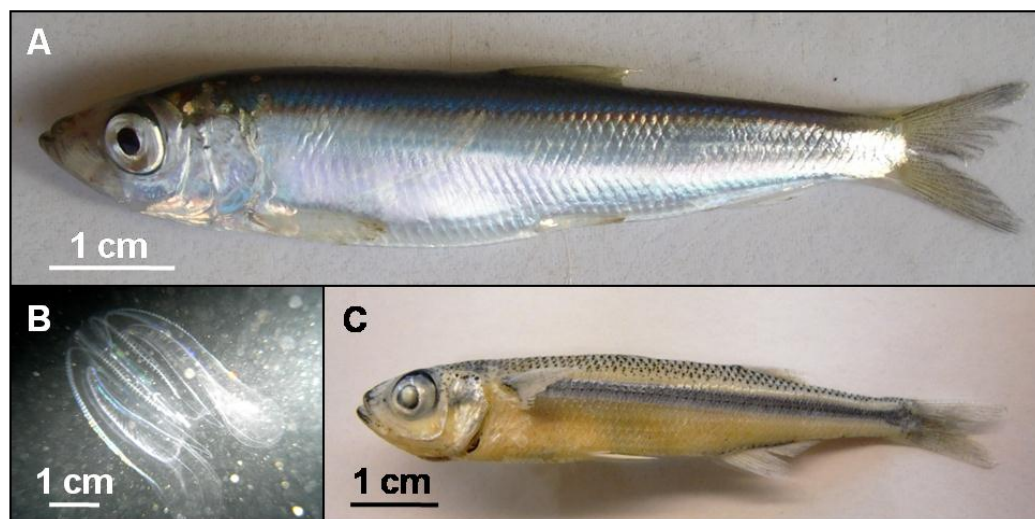


Fig. 1.2 (A) Herring (*Clupea harengus*) (B) Sea walnut (*Mnemiopsis leidyi*) and (C) Sand smelt (*Atherina presbyter*)

#### 1.4 Outline of the study

The objective of the study is to detect possible interactions of alien species with the food web of the Wadden Sea, particularly the upper part of the food web which is represented

by fish. To evaluate which species might interact with each other it was necessary to determine the diets of the common fish species in the area. The first two publications of this study are dedicated to the analysis of the dietary structure of the fish of the Sylt-Rømø bight. For the other two publications two new species in the Sylt-Rømø bight food web, the sea walnut *Mnemiopsis leidyi* (Fig. 1.2B) and the sand smelt *Atherina presbyter* (Fig. 1.2C) were chosen and the possible interactions with a representative of the native fish fauna, the herring *Clupea harengus* (Fig. 1.2A) were analyzed.

- Publication 1:  
Seasonal differences in fish assemblage and feeding guild structure were identified by the means of a fish survey and analysis of the guts of the fish caught. Intertidal and subtidal areas were sampled to check for differences in fish abundance and species composition between these two areas. Dietary overlap between the different fish species was calculated and fish were grouped into feeding guilds.
- Publication 2:  
To add information on distinct trophic positions of fish and the provenance of their food, a stable isotope analysis was performed. Isotopic composition of carbon was used to trace the origin of food. Trophic positions were calculated with nitrogen and the help of an isotopic baseline created with mollusk filter feeder samples. Combining the results with information of Publication 1 conclusions on migration behavior, digestive traits and additional food sources can be drawn.
- Publication 3:  
Feeding interactions between the sea walnut, an invasive ctenophore and native juvenile herring were analyzed. Abundance, diet overlap, prey selectivity and stable isotope composition ( $^{15}\text{N}$ ,  $^{13}\text{C}$ ) of both species were assessed. Furthermore, the potential of competition between the sea walnut and herring was evaluated in a mesocosm experiment. The potential risks for native fish through the sea walnut as food competitor were discussed.
- Publication 4:  
The sand smelt is a Lusitanian fish species that becomes increasingly common in the Wadden Sea. The plankton grazing efficiency of sand smelt was compared to the one of native herring in a mesocosm experiment. Additionally diet overlap and

prey selectivity of this two species were assessed using field samples of three different years. The potential of competition between these two species was discussed.

In a following general discussion a synthesis of the results obtained by the four publications is given. General aspects on the feeding interactions of Wadden Sea fish are discussed. Conclusions on the effects of alien species on the fish food web of the Wadden Sea are drawn.

## 2. The Wadden Sea of the North Sea and the Sylt-Rømø Bight

### 2.1. The Wadden Sea

The Wadden Sea extends from Blåvandshuk, Skallingen, Denmark to Den Helder, Netherlands and includes the estuaries and coastal waters inside and outside the barrier islands (De Jong et al. 1999) (Fig. 2.1). It is 500 km long and the mainland coastal plain covers an area of 24000 km<sup>2</sup> and is therefore one of the largest coherent tidal flat areas in the world (Reise 2005). Since 2009 the Dutch and the German parts of the Wadden Sea are inscribed on the UNESCO World Heritage List.

Wadden Seas are marine areas with a shallow coast under strong influence of the tides (Dittmann 2006). A flat onshore area and a large reservoir of sediments are necessary for the formation of a Wadden Sea area. The formation of the Wadden Sea of the North Sea started about 7500 years ago (Lotze et al. 2005). The rise of the sea level after the last ice age caused an inflow of water into the southern North Sea basin. The increasing influence of the tides on the flat coastal areas entailed a redistribution of sediments which formed the Wadden Sea (Flemming et al. 2002).

Some 1000 years ago men started with the building of dikes for reclamation of land, which are responsible for the appearance of the German Wadden Sea in its present form (Flemming et al. 2002).

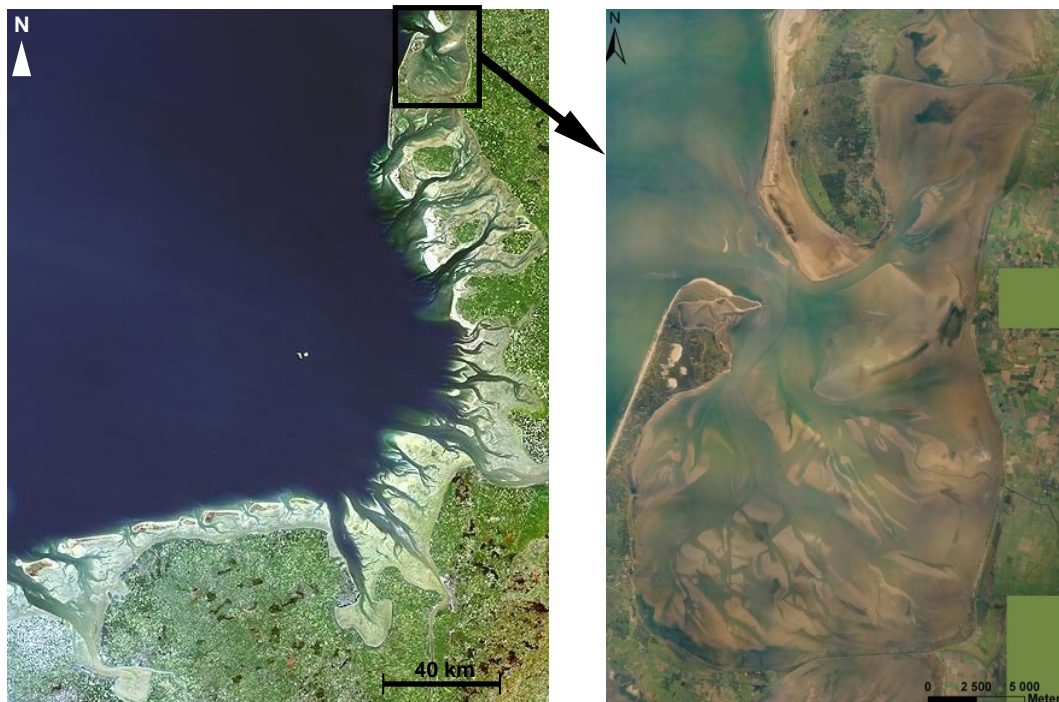


Fig. 2.1 The German Wadden Sea (left) and the Sylt-Rømø bight (right)

## 2.2. The Sylt-Rømø bight

The Sylt-Rømø bight is located in the most northern part of the German Wadden Sea at the border between Germany and Denmark (54° 52` to 55° 10` N, 8° 20` to 8° 40` E) (Fig. 2.1). The basin is enclosed by the islands of Sylt and Rømø and their causeways connecting them to the mainland. The bight covers an area of 407 km<sup>2</sup> in total and is separated into an intertidal area (134 km<sup>2</sup>) and a subtidal area (273 km<sup>2</sup>) (Baird et al. 2004, Gätje and Reise 1998). The subtidal area again can be separated into shallow subtidal flats and tidal gullies. The shallow subtidal flats have a maximum depth of 5 m below low water level and cover an area of 232 km<sup>2</sup>. The deepest parts of the bight are found in the tidal gullies. The three main tidal gullies (Rømø-Dyb, Høyer-Dyb and Lister-Ley) are connected by the Lister Deep between the two islands where maximal depth of 40.5 m below low water level is found. The Lister Deep is the only connection to the North Sea where water is exchanged through the tides. The tidal range is 2 m (Gätje and Reise 1998). On average the basin contains 570x10<sup>6</sup> m<sup>3</sup> of water at low water, 1120x10<sup>6</sup> m<sup>3</sup> at high water and the water residence time is between 19 and 29 days (Asmus and Asmus 2000). The salinity ranges from 27 to 32 psu with the lowest values in winter and the highest in summer. The average water temperature over a year is 9 °C, whereat half year mean in summer season is 15 °C and half year mean in winter season is 4 °C. Nevertheless water temperatures in warm summers reach up to 28 °C in protected shallow subtidal areas and in cold winters the bight is covered by drift ice (Gätje and Reise 1998).

The major part of the Sylt-Rømø bight is covered by sandy sediments. Muddy sediments are restricted to the intertidal areas with very low current, for example close to the causeways and in the Königshafen. *Zostera noltii* sea grass beds, mussel (*Mytilus edulis*) and oyster (*Crassostrea gigas*) beds form characteristic habitats adding structure to the otherwise uniform sandy bottoms. While sea grass beds cover about 15 % of the intertidal areas mussel and oyster beds are restricted to much smaller areas (Baird et al. 2004, Thieltges et al. 2004). The latter are often mixed mussel and oyster beds and may also occur in shallow subtidal areas. Here they are often overgrown by *Sargassum muticum*, a large brown sea weed which forms a dense canopy (Buschbaum et al. 2006).

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### 3. Seasonal variation of assemblage and feeding guild structure of fish species in a boreal tidal basin.

Florian Kellnreitner, Moritz Pockberger, Harald Asmus

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#### Abstract

Species composition, abundance, feeding relationships and guild structure of the fish assemblage in the Sylt-Rømø Bight, a tidal basin in the northern Wadden Sea, were investigated and seasonal differences were identified. Fish were sampled at tidal flats and shallow subtidal areas using a beach seine. A bottom trawl net was used for deeper subtidal areas and tidal gullies. Highest species diversity of fish was observed in summer where 26 species were caught, while the lowest diversity was recorded in winter (17 species). Clear differences in species diversity and abundance were found between shallow areas and deeper parts of the bight. *Clupea harengus* and *Ammodytes tobianus* were the most abundant species in deeper areas, while *Pomatoschistus microps* and *Pomatoschistus minutus* dominated shallower waters. Gut contents of 27 fish species were identified and the guild structure analyzed by UPGMA clustering of niche overlaps. Calanoid copepods (19.9%), *Crangon crangon* (18.2%) and mysid shrimps (8.4%) were the most abundant prey items of all fish species combined. Seven feeding guilds were present in fall and winter, and eight and six in spring and summer, respectively. Fish feeding on calanoid copepods and *C. crangon* were present year round, whereas the occurrence of other guilds varied between seasons. Species composition of prey changed through seasons, and for some fish species, even the feeding mode itself varied with season. Most noticeable, 11 fish species switched guild from one season to another. We found a convergence in summer towards abundant prey items, whereas in winter diet overlap was lower. Our study documents the first investigation of guild structure of almost all fish species present in a Wadden Sea area, and shows that consideration of seasonal differences is essential when determining feeding relationships of fish in temperate areas.

Keywords: feeding habits; diet composition; guild structure; seasonal variation; fish ecology; Wadden Sea; 54° 52' to 55° 10' N, 8° 20' to 8° 40' E;

### 3.1. Introduction

Aggregation of species into feeding guilds is a common practice in food web studies. It helps to disentangle complex trophic interactions into clearly arranged pathways and to structure a community into fewer groups with similar food requirements. The first use of the term guild was adapted by Root (1967) and defined as “a group of species that exploit the same class of environmental resources in a similar way”. This refers to the sharing of resources by multiple species in a competitive context (Blondel, 2003). Elliott et al. (2007) consider the guild approach as a good method to compare estuarine and transitional habitats worldwide. They proposed three groups of functional guilds based on the use of the habitat, reproductive mode and feeding mode of a given species. Besides arbitrary and intuitive designation of guilds, some objective methods for guild identification have been made such as the ones applied by Lawlor (1980) or Jaksić and Medel (1990).

In recent years much has been done to identify feeding guild structures of fish communities worldwide (Muñoz and Ojeda, 1997; Garrison and Link, 2000; Wennhage and Pihl, 2002; Boyle and Horn, 2006; Castellanos-Galindo and Giraldo, 2008; Reum and Essington, 2008; Green et al., 2009; Hajisamae, 2009). However, work on feeding guilds of fish species in the Wadden Sea is scarce (Elliott and Dewailly, 1995; Herrmann et al., 1998b). The Wadden Sea, a UNESCO world heritage area since 2009, is widely known as a nursery ground for commercially important fish of the North Sea and provides habitat for small sized fish species (Rauck and Zijlstra, 1978; Zander and Hartwig, 1982; Polte and Asmus, 2006). Species composition and abundance change seasonally (Greenstreet et al., 1997; Herrmann et al., 1998a), yet have also been affected by human activities and climate change in the last centuries (Lozán et al., 1994; Lotze, 2005).

Particularly in the 1980s and 1990s, much work has focused on the consumption and feeding habits of fish species in the North and Wadden Sea (Daan, 1973; Robb and Hislop, 1980; Last, 1987; Hamerlynck and Hostens, 1993; Herrmann et al., 1998b; Hostens and Mees, 1999). There have been some attempts to construct food webs including fish (Baird et al., 2004, 2007), but the contributions based on feeding guilds were often focused on the North Sea (Greenstreet et al., 1997). Food webs constructed by Greenstreet et al. (1997) for different quarters of the year focused mainly on the biomass of fish and mass flows. Elliott and Dewailly (1995) compared different European estuarine and Wadden Sea areas. Both studies derived feeding habits of fish and guild membership from literature data of the 1980s and 1990s. Herrmann et al. (1998a, b)

investigated abundance and gut contents of the dominant fish species of the Sylt-Rømø Bight, where species were divided into three groups according to their size and preferred prey. To our knowledge so far no work had included all fish present in a Wadden Sea area in the different seasons of a year in a study on feeding guilds.

Our investigation of guild structure of fish species in the Sylt-Rømø Bight was based on gut content data collected within one year. We predicted differences in feeding guild structure based on expected seasonal changes in prey abundance, fish abundance and fish species composition, and tested this hypothesis using re-sampling methods (e.g. bootstrapping; Jaksic and Medel, 1990). Such methods provide a realistic description of prey overlap and were used to identify: (a) possible interactions between different fish species, (b) important food resources for fish, and (c) the role of season for guild composition and variability of key prey items. Our study shows the importance of accounting for seasonal changes in food web models, and thus represents a basis for further investigations of trophic fish ecology in the Wadden Sea area.

## 3.2. Material and Methods

### 3.2.1. Study area

The Sylt-Rømø Bight is part of the Wadden Sea and is located at the border of Germany and Denmark (54° 52' to 55° 10' N, 8° 20' to 8° 40' E). It is delimited by the islands Rømø in the North and Sylt in the South-West, and is connected to the North Sea through a 2.8 km wide channel between the islands. The bight covers an area of 406 km<sup>2</sup>, including a tidal flat area of 135 km<sup>2</sup>. The subtidal area is divided into two components: a shallow region ranging from the low tide line to a depth of 5 m (231 km<sup>2</sup>), and a deeper region consisting of tidal gullies deeper than 5 m (40 km<sup>2</sup>). Mean depth at high tide is 4.2 m at an average tidal range of 2 m. Tides are semidiurnal and 8 to 12% of water from the bight exchanges with the adjacent North Sea (Fast et al., 1999; Asmus and Asmus, 2000). A more detailed description of the Sylt-Rømø Bight is given in Gätje and Reise (1998).

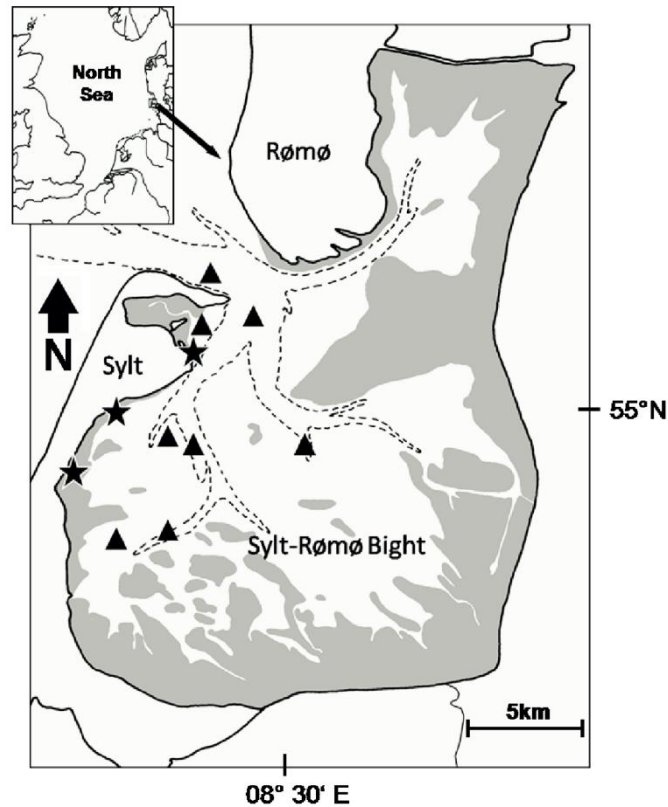


Fig. 3.1 Map of study area. Stars indicate stations for beach seine catches, and triangles for bottom trawl net catches. Grey areas represent tidal flats and dashed lines indicate main tidal gullies (shown only for Sylt-Rømø Bight).

### 3.2.2. Sampling

Sampling took place monthly from July 2008 to June 2009, the exact dates depending on tides and weather conditions. Stations were chosen haphazardly to provide good geographic coverage of the German part of the bight (Fig. 3.1). Two different sampling strategies were pursued. Tidal flats and shallow subtidal areas were sampled using a beach seine, and a bottom trawl was used for deeper subtidal areas and tidal gullies. The beach seine measured 12 m in width and 2 m in height with a mesh size of 6 mm for the wings and 4 mm for the cod end. Three points were sampled with the beach seine; at each point one haul was performed in the intertidal area and one in the shallow subtidal area. Sampling was performed during daylight hours at high tide in intertidal areas and during low tide in subtidal areas. An area of approximately 180 m<sup>2</sup> was covered with each haul.

The mouth opening of the bottom trawl measured 7 m in width and 3 m in height. Mesh size was 32 mm for the wings and 6 mm for the cod end. To sample the pelagic zone at stations with greater depths, towing lines of the bottom trawl were shortened. At these stations, a bottom haul and a pelagic haul were performed. The net was towed for 15 min at approximately 2 knots, and positions were taken by Global Positioning System (GPS) to calculate distances. Catches were sorted into species, counted and measured to the nearest 0.5 cm. A subsample was taken when large samples of a species were present. Up to 12 individuals of each species were randomly selected from the catches each month for gut content analysis. Individuals were anesthetized using MS 222 and sacrificed by destruction of the brain. Individuals were preserved in 5% buffered formalin solution for at least 2 days. Larger specimens were dissected on board and guts were preserved in 5% buffered formalin solution.

### 3.2.3. Gut content analysis

Individuals were soaked in freshwater for at least 24 h before dissection. Fish were measured to the nearest mm and weighted to the nearest 0.1 g. Only stomach contents were analyzed. If the stomach was not clearly distinct the whole gut was analyzed. This was the case for gobies of the genus *Pomatoschistus* and for *Syngnathus rostellatus*. Gut contents were identified to the lowest taxonomic level possible. Unidentifiable copepods were assumed to be the same taxon as identified copepods in the gut and their number was added to identified copepods in the present proportion of identified copepods. Parasitic organisms were excluded from calculations.

### 3.2.4. Data analysis

Fish species with a total catch number less than 5 individuals and only caught once at one station were excluded from analysis. This included *Anguilla anguilla*, *Aphia minuta*, *Callionymus lyra*, *Chelon labrosus*, *Lampetra fluviatilis*, *Salmo trutta*, *Solea solea*, *Spinachia spinachia* and *Triglia lucerna*.

Catch data was standardized to individuals 1000 m<sup>-2</sup>. Weighted means were calculated by considering the different depth areas of the bight by surface. The total abundance within guilds was determined by summing up the abundance of their members. Estimates of gear efficiency were not included in calculations.

Trophic indices were used to describe the importance of the different food types found in the stomachs of the different fish species. A numerical index was chosen because the major part of food items in the stomach of an analyzed individual was in the same size

range (Hyslop, 1980). The numerical index gives the proportion (%) of the items of each prey category relative to the total number in a stomach and was calculated for each analyzed individual. The index of Occurrence (IO) gives the percent of individuals with non empty guts which fed on a certain prey item. Vacuity index (VI) was calculated as a percentage of empty guts relative to the total number of examined guts. Mean number of prey types refers to the mean number of ingested prey types of each fish species. Seasons were defined as follows: spring - from March to May (mean water temperature 5.5-13.1°C), summer - from June to August (14.0-19.0°C), fall - from September to November (14.0-6.6°C) and winter from December to February (3.6-0.9°C). Fish with a total length less than 50% of the recorded maximal total length were categorized as small. In each season/size class only species with at least 3 individuals with non empty stomachs were taken into account to calculate diet overlap. Diet overlaps were calculated with mean values of numerical index per fish species per prey after Pianka's (1973) niche overlap index. This index results in values between 0 and 1 (or between 0 and 100%), signifying overlap of food resource use of two consumers from zero to complete overlap. The resulting diet similarity matrix was subjected to a UPGMA analysis (Unweighted Pair Group Method with Arithmetic mean). The significant similarity level for objective guild recognition was found by applying the bootstrapping method of Jaksic and Medel (1990). Raw data was reshuffled using Lawlor's RA 4 algorithm (Lawlor, 1980) retaining zero values in their original position and reassigning remaining values within columns. Data were reshuffled 250 times, and each time a diet similarity matrix was constructed (Jaksic and Medel, 1990). The resulting similarity values were used to create a frequency distribution histogram to determine the critical value, beyond which the probability of occurrence of similarities is <5%. UPGMA analysis was performed using XLSTAT (2009) software, while the bootstrapping procedure was done with the PopTool add-in (Hood, 2009). The resulting guilds were subjected to a similarity percentage analysis (SIMPER) using the statistical software PRIMER 6 (Clarke and Gorley, 2006).

### 3.3. Results

#### 3.3.1. Abundance and species composition

The bight was dominated by juvenile and small sized fish species seldom exceeding 20 cm in length (Table 3.1). However, large adult specimens of *Belone belone* (45-60.5 cm) were caught in spring and summer.

Table 3.1 Mean total lengths (TL) in centimeters with size range in parentheses of fish caught during sampling.

Species	TL (cm)				
	Summer 08	Fall 08	Winter 08/09	Spring 09	Summer 09
<b>Beach Seine</b>					
<i>Ammodytes tobianus</i>	6.46 (5.5-11)	6.95 (6-8)	-	7.92 (7.5-8.5)	9.25 (6-11.5)
<i>Atherina presbyter</i>	5.88 (2.5-8)	7.47 (5.5-9.5)	-	-	7.00
<i>Ciliata mustela</i>	6.33 (5.5-7.5)	-	-	-	-
<i>Clupea harengus</i>	5.49 (4-8.5)	8.00	9.63 (7.5-11.5)	5.94 (5-7.5)	8.24 (5.5-10)
<i>Gasterosteus aculeatus</i>	6.07 (3-7.5)	-	-	5.89 (3.5-6.5)	-
<i>Hyperoplus lanceolatus</i>	20.00	-	-	-	-
<i>Liparis liparis</i>	-	-	-	-	5.20 (5-5.5)
<i>Merlangius merlangus</i>	-	-	-	-	7.38 (7-7.5)
<i>Myoxocephalus scorpius</i>	4.50	-	-	3.42 (3-4)	4.64 (4-5.5)
<i>Osmerus eperlanus</i>	-	-	8.50	-	-
<i>Platichthys flesus</i>	-	11.25 (10.5-12)	-	11.13 (8-13.5)	11.00 (5-19)
<i>Pleuronectes platessa</i>	6.72 (5.5-8)	12.50 (12-13)	-	2.75 (1-11)	6.06 (3.5-10)
<i>Pomatoschistus microps</i>	3.07 (1-5.5)	3.53 (2-6)	5.06 (3-4.5)	4.56 (3.5-6)	3.24 (1-6.5)
<i>Pomatoschistus minutus</i>	4.96 (2-8)	6.42 (3.5-9)	5.50	5.15 (4-8.5)	4.35 (2-8)
<i>Syngnathus rostellatus</i>	11.12 (6.5-14.5)	9.90 (8-12)	10.50	9.50 (8-11)	11.20 (6.5-14)
<i>Trachurus trachurus</i>	7.50	-	-	-	-
<i>Zoarces viviparus</i>	9.63 (9-10)	-	13.50 (4-26)	9.19 (5.5-18)	11.00
<b>Bottom Trawl</b>					
<i>Agonus cataphractus</i>	9.46 (4-12)	12.31 (6-20)	11.45 (7.5-15)	8.15 (3-13)	5.36 (3-13.5)
<i>A. tobianus</i>	13.15 (8.5-20)	12.11 (6-18.5)	12.82 (6-16)	14.21 (5.5-19.5)	10.51 (8-18)
<i>Belone belone</i>	52.25 (52-52.5)	10.50	-	54.88 (45-60.5)	53.39 (5-60)
<i>C. mustela</i>	8.00	13.01 (11-14)	-	-	-
<i>C. harengus</i>	8.15 (5-11.5)	8.56 (5.5-14)	8.47 (5-14)	6.65 (4-12.5)	8.46 (4-10.5)
<i>Cyclopterus lumpus</i>	-	5.24 (3.5-12)	5.15 (4-8)	-	-
<i>Engraulis encrasicolus</i>	5.27 (3.5-6)	-	-	15.19 (13.5-17)	4.50
<i>Gadus morhua</i>	8.13 (7-10)	13.75 (13-14.5)	14.02 (11.5-15.5)	6.96 (4-17)	6.80 (6-10.5)
<i>G. aculeatus</i>	5.62 (5.5-6)	5.62 (3-7)	5.34 (3-7)	5.48 (3-7)	6.34 (2-7)
<i>H. lanceolatus</i>	17.47 (12.5-29)	24.50 (22-27)	-	13.24 (5-24.5)	21.71 (14-26)
<i>Limanda limanda</i>	5.99 (5-7)	12.75 (4.5-27.5)	16.19 (7-28.5)	13.09 (11.5-15.5)	13.63 (13-14.5)
<i>L. liparis</i>	6.97 (6-7.5)	7	-	3.59 (2.5-12.5)	4.93 (3.5-7)
<i>M. merlangus</i>	8.89 (5.5-16.5)	18.72 (13.5-30)	23.32 (15-28.5)	5.33 (5-6)	7.92 (5-17)
<i>Mullus surmuletus</i>	5.74 (5-6)	-	-	-	6.00
<i>M. scorpius</i>	10.72 (6-16)	11.83 (10.5-13.5)	11.94 (9-15)	4.59 (2-13)	5.32 (3.5-15.5)
<i>O. eperlanus</i>	7.33 (6.5-8)	9.54 (5.5-16)	9.15 (5.5-15.5)	11.86 (8-13.5)	15.99 (5-19.5)
<i>Pholis gunnellus</i>	11.82 (11-14.5)	9.15 (8.5-10)	-	11.56 (9-15.5)	12.88 (10.5-16.5)
<i>P. flesus</i>	18.62 (17.5-20)	18.21 (11.5-19)	10.96 (8-16.5)	14.83 (4.5-21.5)	13.17 (10-16)
<i>P. platessa</i>	8.41 (5-10.5)	8.27 (7-12.5)	10.19 (6-19)	11.48 (2.5-22)	6.07 (4-12.5)
<i>Pomatoschistus lozani</i>	5.13 (4.5-6)	-	-	-	-
<i>P. microps</i>	-	4.71 (2.5-6.5)	4.17 (3-5.5)	-	-
<i>P. minutus</i>	6.44 (3.5-8.5)	6.40 (3.5-9.5)	6.68 (4.5-8.5)	6.86 (3-9)	6.48 (4-8.5)
<i>Sprattus sprattus</i>	10.56 (7.5-12)	6.86 (4.5-12.5)	6.58 (4.5-14)	7.78 (4.5-13.5)	9.22 (6.5-11.5)
<i>S. rostellatus</i>	10.81 (5-17.5)	8.92 (5-17)	9.43 (7.5-13)	9.72 (6.5-16.5)	11.88 (5-16.5)
<i>T. trachurus</i>	6.61 (5-9)	-	-	-	4.82 (3-7.5)
<i>Z. viviparus</i>	11.10 (10-18)	-	14.19 (10.5-24.5)	14.92 (13-22)	11.23 (9-26)

Highest overall abundances were found in summer in beach seine catches and in spring in bottom trawl catches. Abundances were higher in beach seine catches than in bottom trawl catches. In beach seine catches, *Pomatoschistus microps* and *Pomatoschistus minutus* were the most abundant species. There was a pronounced decline in total fish abundance in shallow areas in winter. The most abundant species in bottom trawl catches were *Clupea harengus* and *Ammodytes tobianus* (Fig. 3.2). *C. harengus* was abundant throughout the year, whereas the abundance of *A. tobianus* diminished in fall and was close to zero in winter.

A total of 27 fish species were caught. The number of species ranged from 26 species in summer to 17 species in winter. During spring and fall, 21 and 22 fish species were caught, respectively. During the entire study period, 26 species were present in bottom trawl catches and 17 in beach seine catches. The only species being exclusively present in beach seine catches was *Atherina presbyter* during summer and fall (Fig. 3.2).

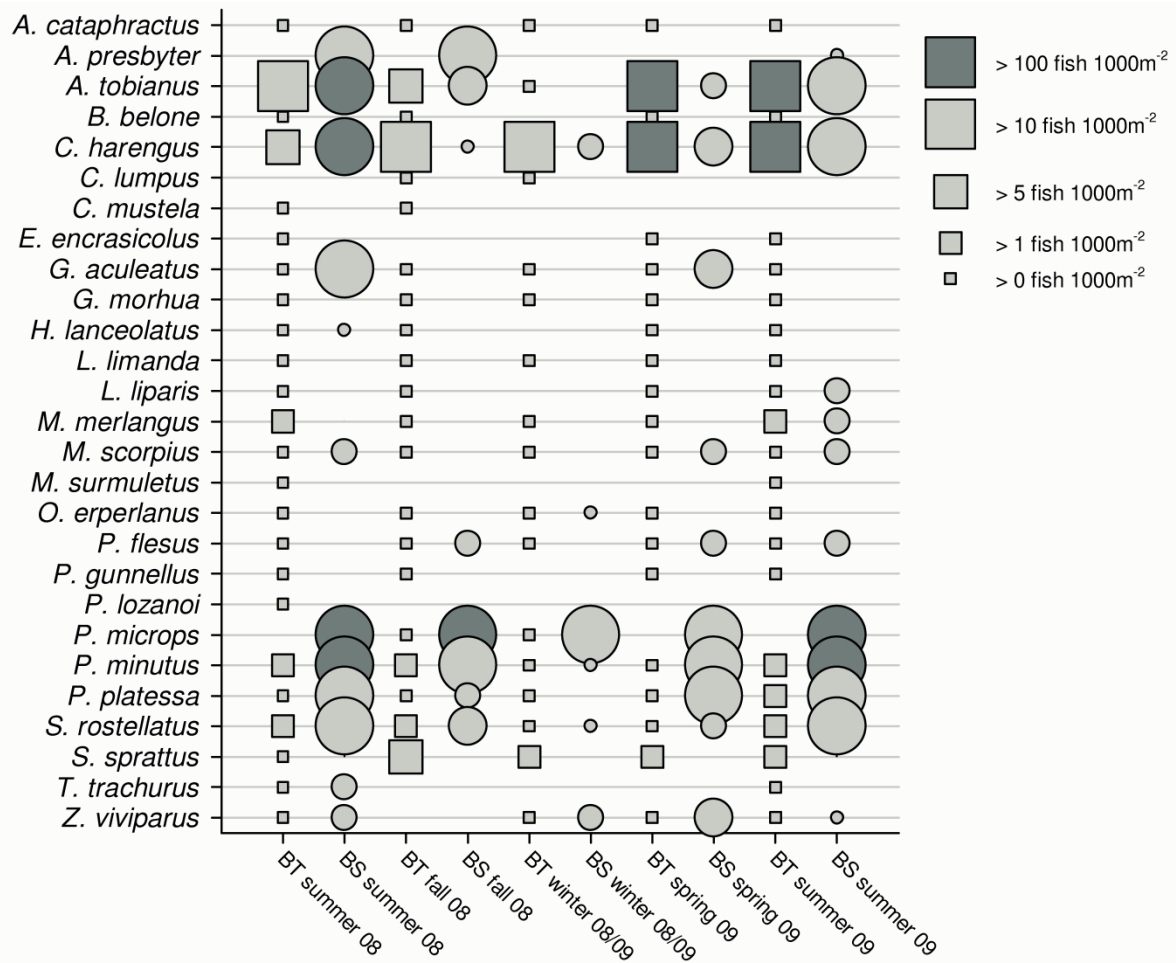


Fig. 3.2 Fish abundances resulting from catches with bottom trawls (BT) and beach seines (BS) in different seasons. Squares represent bottom trawl catches and circles depict beach seine catches. Full notations of scientific names are given in Table 1.

### 3.3.2. Feeding ecology

Gut contents of 1256 fish were analyzed, of which 273 guts were empty. The highest percentage of empty guts was found in fall and winter, and the lowest in summer. Especially *A. tobianus*, *Gasterosteus aculeatus* and *Pleuronectes platessa* showed high



percentages of empty guts in fall and winter (Table 3.2). The only species being present in samples throughout the year in high numbers with a low Vacuity index were *C. harengus* and *Sprattus sprattus* (Fig. 3.2, Table 3.2).

A total of 73 prey types could be identified in the guts of the fish. Examination of overall relative gut content by fish revealed calanoid copepods as the most dominant prey (19.9%). *Crangon crangon* (18.2%) ranked second followed by mysid shrimp (8.4%), amphipods (8.0%), harpacticoid copepods (3.7%), cypris larvae (3.6%), neridid polychaetes (3.4%) and undefined polychaetes (2.5%). The other 65 prey types comprised 32.3% of the gut contents. The mean number of prey types ranged from 1.0 for *Pleuronectes platessa* in winter to 7.4 for *A. presbyter* in fall. More than half of the fish species sampled in the different seasons demonstrated a mean of less than 2.3 prey types (Table 3.2).

Table 3.2 Numerical index of food types for fish in the Sylt-Rømø Bight and index of occurrence (IO in bold) per guild in different seasons. All guild determining prey items are represented, with the rest grouped as other (oth.). Number of individuals with full gut (n), total length of fish with full guts (TL) in cm with standard deviation, mean number of prey types (x prey) per species, Vacuity index (VI) in %, and means per guild (bold) are shown. Values are rounded and may exceed 100%. amp. – Amphipoda, bif. – Bivalvia siphon, bip. – Bivalvia parts, cal. – calanoid copepods, clu. – Clupeidae, cra. – *C. crangon*, cte. – Ctenophora, cyp. – cypris larvae, ens. – *Ensis* sp., fis. – not defined fish, har. – harpacticoid copepods, ido. – *Idotea linearis*, mys. – mysid shrimp, ner. – Nereididae, pol. – not defined Polychaeta. For guild abbreviations see Fig. 3.4.

	guild	species	n	TL (cm)	x prey	VI (%)	amp.	bif.	bip.	cal.	clu.	cra.	cte.	cyp.	ens.	fis.	har.	ido.	mys.	ner.	pol.	zoe.	oth.
Spring	CRA	<i>A. cataphractus</i>	7	11.0±0.9	1.7	0	16.7	7.1	-	-	-	67.9	-	-	-	-	-	-	-	-	-	-	8.3
		<i>G. morhua</i> L	3	14.8±1.5	1.7	0	-	-	-	-	-	-	72.2	-	-	-	-	-	-	-	27.8	-	-
		<b>x</b>			<b>1.7</b>	<b>0</b>	<b>8.3</b>	<b>3.6</b>	-	-	-	<b>70</b>	-	-	-	-	-	-	-	<b>13.9</b>	-	-	<b>4.2</b>
		<b>IO</b>				<b>0.1</b>	<b>0.1</b>	-	-	-	<b>0.9</b>	-	-	-	-	-	-	-	-	<b>0.3</b>	-	-	
	HAR	<i>P. microps</i>	24	4.5±0.6	2.2	17.2	7.7	-	-	-	-	23.6	-	6	-	-	25.6	-	9.5	-	4.8	-	22.9
		<b>IO</b>				<b>0.2</b>	<b>0.2</b>	-	-	-	-	<b>0.4</b>	-	<b>0.2</b>	-	-	<b>0.4</b>	-	<b>0.2</b>	-	<b>0.1</b>	-	
	AMP	<i>G. aculeatus</i>	7	5.8±0.4	2.1	0	50.1	-	-	24.7	-	2	-	5.7	-	-	-	-	-	-	16.7	-	0.8
		<b>IO</b>				<b>0.9</b>	<b>0.9</b>	-	-	<b>0.3</b>	-	<b>0.1</b>	-	<b>0.1</b>	-	-	-	-	-	-	<b>0.4</b>	-	
	FIS	<i>H. lanceolatus</i> L	6	19.9±2.8	1.7	40	-	-	-	-	8.3	-	-	17.5	-	41.7	-	-	0.8	-	-	-	31.7
		<b>IO</b>				<b>0.2</b>	<b>0.2</b>	-	-	<b>0.2</b>	-	<b>0.3</b>	-	<b>0.5</b>	-	<b>0.5</b>	-	<b>0.2</b>	-	<b>0.2</b>	-	-	
	BIP	<i>P. minutus</i>	21	7.4±0.9	2.1	16	3.4	9.5	22.8	2.3	-	2.9	-	7.3	-	-	10.6	-	4.8	-	<0.1	-	36.5
		<b>IO</b>				<b>0.2</b>	<b>0.1</b>	<b>0.4</b>	<b>&lt;0.1</b>	<b>&lt;0.1</b>	-	<b>0.1</b>	-	<b>0.2</b>	-	<b>0.2</b>	-	<b>0.2</b>	-	<b>&lt;0.1</b>	-	<b>&lt;0.1</b>	-
	NER	<i>P. flesus</i>	7	13.5±2.9	1.3	46.7	-	-	-	-	-	14.3	-	-	-	-	-	-	-	65.1	15.9	-	4.8
		<i>P. platessa</i> L	5	13.1±4.0	1.6	16.7	-	11.4	38.9	-	-	-	-	-	-	-	-	-	-	40	0.6	-	9
		<b>x</b>			<b>1.4</b>	<b>31.7</b>	-	<b>5.7</b>	<b>19.5</b>	-	-	<b>7.1</b>	-	-	-	-	-	-	-	<b>52.5</b>	<b>8.2</b>	-	<b>6.9</b>
		<b>IO</b>				<b>0.2</b>	<b>0.1</b>	<b>0.2</b>	-	-	<b>0.1</b>	-	-	-	-	-	-	-	-	<b>0.6</b>	<b>0.2</b>	-	
	CLU	<i>B. belone</i>	5	54.5±6.1	2	0	-	-	-	-	30	1.5	-	-	-	3.3	-	-	-	21.5	13.3	-	30.3
		<b>IO</b>				<b>0.4</b>	<b>0.4</b>	-	-	<b>0.4</b>	<b>0.2</b>	-	-	-	<b>0.2</b>	-	-	-	<b>0.4</b>	<b>0.4</b>	-	-	
	CAL	<i>A. tobianus</i>	24	13.7±2.1	4.2	20	1.5	-	-	21.8	-	-	-	18.5	-	-	9.3	-	14.6	-	-	0.3	34
		<i>C. harengus</i>	18	8.4±1.5	3.9	5.3	-	-	-	51.8	-	-	-	9.4	-	-	0.5	-	10.3	-	-	0.2	27.8
		<i>E. encrasicolus</i> L	10	14.7±0.8	6.4	0	-	-	-	30	-	0.4	-	4.5	-	-	-	-	2.8	-	-	59.9	2.4
		<i>H. lanceolatus</i> S	15	9.9±0.8	2.7	21.1	-	-	-	72.5	-	-	-	9.8	-	-	1	-	0.4	-	-	-	16.3
		<i>M. merlangus</i> S	9	4.8±0.5	3	0	13.1	-	-	34.9	-	-	-	2.8	-	-	0.7	-	8.8	-	-	38.9	0.8
		<i>P. lozanoi</i>	6	4.9±1.2	3	25	2.8	-	-	17.4	-	-	-	22.4	-	-	7.5	-	16.7	-	-	-	33.2
		<i>S. sprattus</i>	24	7.8±1.6	3.9	20	0.1	-	-	68.7	-	-	-	13.4	-	-	7.5	-	0.1	-	-	0.4	9.9
		<i>S. rostellatus</i>	17	10.0±1.4	3.1	41.4	4	-	-	57.9	-	1.5	-	1.3	-	0.2	-	-	12	-	-	1.6	21.4
		<b>x</b>			<b>3.8</b>	<b>16.6</b>	<b>2.7</b>	-	-	<b>44.4</b>	-	<b>0.2</b>	-	<b>10.3</b>	-	<b>&lt;0.1</b>	<b>3.3</b>	-	<b>8.2</b>	-	-	<b>12.7</b>	<b>18.2</b>
		<b>IO</b>				<b>0.1</b>	<b>0.1</b>	-	-	<b>0.8</b>	-	<b>&lt;0.1</b>	-	<b>0.5</b>	-	<b>&lt;0.1</b>	<b>0.2</b>	-	<b>0.4</b>	-	-	<b>0.3</b>	

Table 3.2 continued

	guild	species	n	TL (cm)	x prey	VI (%)	amp.	bif.	bip.	cal.	clu.	cra.	cte.	cyp.	ens.	fis.	har.	ido.	mys.	ner.	pol.	zoe.	oth.	
Summer	CRA	<i>A. cataphractus</i>	17	11.1±0.8	1.3	9.5	16.7	-	6.3	-	-	57.3	-	-	-	-	-	-	2.1	-	-	-	17.7	
		<i>L. liparis</i>	10	5.6±0.9	1.6	9.1	-	-	-	8.1	-	-	35	-	-	-	-	-	-	23.6	-	-	-	33.3
		<i>M. merlangus</i> L	16	12.7±2.0	1.9	5.9	-	-	5	-	-	-	49.2	-	-	6.3	3.1	-	-	15.3	1.6	-	-	19.5
			<i>M. scorpius</i> L	7	13.7±1.3	1.1	22.2	-	-	-	-	95.2	-	-	-	-	-	-	-	-	-	-	-	4.8
	CRA	<i>M. scorpius</i> S	10	5.9±1.5	1.8	9.1	15.7	-	-	-	-	58.3	-	3.8	-	-	-	-	-	10	-	-	-	12.3
		<i>O. eperlanus</i> L	6	15.7±2.3	2	0	-	-	-	-	2.8	62.5	-	-	-	8.3	-	-	-	13.9	-	-	-	12.5
		<i>P. microps</i>	5	5.4±0.3	3.3	0	-	-	-	-	-	51.9	-	-	-	-	-	-	-	-	2.8	7.8	-	37.5
		<i>P. minutus</i>	29	6.7±1.0	1.9	3.3	-	-	-	-	-	26.8	-	4.8	1.7	-	-	-	-	12.1	-	4.6	-	50
		<b>x</b>			<b>1.9</b>	<b>7.4</b>	<b>4</b>	-	<b>1.4</b>	<b>1</b>	<b>0.3</b>	<b>54.5</b>	-	<b>1.1</b>	<b>1</b>	<b>1.4</b>	-	-	-	<b>9.6</b>	<b>0.5</b>	<b>1.5</b>	-	<b>23.5</b>
		<b>IO</b>					<b>0.1</b>	-	<b>&lt;0.1</b>	<b>&lt;0.1</b>	<b>&lt;0.1</b>	<b>0.8</b>	-	<b>&lt;0.1</b>	<b>&lt;0.1</b>	<b>&lt;0.1</b>	-	-	-	<b>0.2</b>	<b>&lt;0.1</b>	<b>0.1</b>	-	
	AMP	<i>G. morhua</i> L	3	8.9±1.0	2.3	0	48.1	-	-	-	-	16.7	-	-	-	-	-	-	-	3.7	-	-	-	31.5
		<i>G. morhua</i> S	8	7.3±0.7	2.9	0	48.9	-	0.2	-	-	9	-	0.2	-	-	-	-	-	0.8	-	4.2	-	36.7
		<i>M. merlangus</i> S	12	7.6±1.4	2.8	0	20.7	-	-	0.5	-	13.7	-	-	-	-	-	-	-	22.6	-	0.5	0.4	41.5
		<i>M. surmuletus</i>	6	5.7±0.3	2	14.3	42.6	-	-	-	-	3.8	-	-	-	-	-	-	-	23.9	-	-	-	29.6
		<i>P. gunnellus</i>	6	12.6±1.8	2.2	14.3	81.1	-	-	-	-	1.3	-	-	-	-	8.5	-	-	1.3	-	-	-	7.8
		<i>P. platessa</i> S	22	6.8±1.0	2.5	15.4	22.6	-	-	-	-	12.3	-	2.2	6.5	-	5.9	-	-	5	-	30.9	-	14.6
		<i>Z. viviparus</i>	6	13.7±2.7	4.7	37.5	41.1	-	8.5	-	-	-	-	2.2	1.9	-	3.3	-	-	-	-	0.5	-	42.5
			<b>x</b>		<b>2.8</b>	<b>11.6</b>	<b>43.6</b>	-	<b>1.3</b>	<b>0.1</b>	-	<b>8.1</b>	-	<b>0.7</b>	<b>1.2</b>	-	<b>2.5</b>	-	<b>8.2</b>	-	<b>5.1</b>	<b>0.1</b>	<b>29.2</b>	
			<b>IO</b>				<b>0.7</b>	-	<b>0.1</b>	<b>&lt;0.1</b>	-	<b>0.3</b>	-	<b>0.1</b>	<b>&lt;0.1</b>	-	<b>0.1</b>	-	<b>0.3</b>	-	<b>0.1</b>	<b>&lt;0.1</b>	-	
	FIS	<i>H. lanceolatus</i> L	7	19.0±4.7	2.9	22.2	-	-	-	7.6	21.4	15.1	-	-	-	16.5	-	-	-	13.5	-	-	5.6	20.4
		<b>IO</b>					-	-	-	<b>0.1</b>	<b>0.3</b>	<b>0.4</b>	-	-	-	<b>0.4</b>	-	-	-	<b>0.6</b>	-	-	<b>0.3</b>	
	MYS	<i>L. limanda</i> S	9	6.2±0.3	1.1	15.4	1.1	-	-	-	-	-	-	-	-	-	-	-	-	62.5	18.2	18.2	-	-
		<i>T. trachurus</i>	10	6.9±0.9	1.1	0	-	-	-	-	-	2.5	-	-	-	-	-	-	-	97.5	-	-	-	-
<b>x</b>				<b>1.1</b>	<b>7.7</b>	<b>0.6</b>	-	-	-	-	<b>1.3</b>	-	-	-	-	-	-	-	<b>80</b>	<b>9.1</b>	<b>9.1</b>	-	-	
		<b>IO</b>				<b>0.1</b>	-	-	-	<b>0.1</b>	-	-	-	-	-	-	-	-	<b>0.9</b>	-	<b>0.1</b>	-		
ENS	<i>P. platessa</i> L	3	12.5±3.9	1.7	25	-	-	-	-	-	-	-	-	50	-	-	-	-	16.7	16.7	-	-	16.7	
	<b>IO</b>					-	-	-	-	-	-	-	-	-	<b>0.7</b>	-	-	-	<b>0.3</b>	<b>0.3</b>	-	-		
CAL	<i>A. tobianus</i>	26	13.3±2.0	7	13.3	0.1	-	-	77.6	-	-	-	9.6	-	-	0.2	-	-	4.9	-	0.2	0.3	7.1	
	<i>A. presbyter</i>	9	6.3±0.5	5.3	10	0.5	-	-	67.4	-	<0.1	-	1.6	-	-	-	-	-	0	0.8	-	0.2	29.5	
	<i>C. harengus</i>	32	8.1±0.5	3.8	0	1.2	-	-	73.8	-	0.6	-	7.2	-	3.3	0.6	-	-	4.7	-	0.6	<0.1	7.9	
		9	5.5±0.4	4	10	-	-	-	36.8	-	-	-	0.2	-	-	-	-	-	7	-	-	-	56	
	<i>S. sprattus</i>	23	9.9±1.1	4.7	0	<0.1	-	-	88.9	-	<0.1	-	7.8	-	<0.1	-	-	-	1.6	-	0.1	0.2	1.2	
	<i>S. rostellatus</i>	30	12.6±1.2	4.1	0	3.3	-	-	68.9	-	<0.1	-	0.3	-	<0.1	-	<0.1	<0.1	4.1	-	-	1.7	21.6	
	<b>x</b>			<b>4.8</b>	<b>5.6</b>	<b>0.9</b>	-	-	<b>68.9</b>	-	<b>0.1</b>	-	<b>4.5</b>	-	<b>0.6</b>	<b>0.1</b>	<b>&lt;0.1</b>	<b>3.7</b>	<b>0.1</b>	<b>0.2</b>	<b>0.4</b>	<b>0.4</b>	<b>20.6</b>	
		<b>IO</b>				<b>0.3</b>	-	<b>1</b>	-	<b>&lt;0.1</b>	-	<b>0.5</b>	-	<b>0.1</b>	<b>0.1</b>	<b>&lt;0.1</b>	<b>0.4</b>	<b>0.1</b>	<b>0.1</b>	<b>0.1</b>	<b>0.2</b>			
Fall	CRA	<i>A. cataphractus</i>	12	11.7±1.4	1.1	14.3	12.5	-	-	-	-	70.8	-	-	-	-	-	-	-	-	-	-	16.7	
		<i>C. mustella</i>	7	12.9±0.8	1.7	0	2.4	-	-	-	-	49.2	-	-	-	-	-	-	-	-	2.9	-	-	45.5
		<i>M. merlangus</i> L	9	18.7±4.8	1.2	0	-	-	33.3	-	6.5	52.8	-	-	-	-	-	-	-	7.4	-	-	-	
		<i>M. scorpius</i> L	10	11.0±0.9	2.1	0	-	-	-	-	74.7	-	-	-	-	-	-	-	-	-	-	-	25.3	
		<i>O. eperlanus</i> S	5	8.6±0.5	2.4	20	14.7	5	-	5	-	44	5	-	-	-	-	-	17.3	-	-	-	9	
		<i>P. minutus</i>	24	6.9±0.8	1.6	20	9.7	10.4	-	2.7	-	18.1	-	-	-	4.2	4.7	-	12.5	-	1.4	-	36.3	
		<b>x</b>			<b>1.7</b>	<b>9.1</b>	<b>6.5</b>	<b>2.6</b>	<b>5.6</b>	<b>1.3</b>	<b>1.1</b>	<b>51.6</b>	<b>0.8</b>	-	-	<b>0.7</b>	<b>0.8</b>	-	<b>6.2</b>	<b>0.5</b>	<b>0.2</b>	-	<b>22.2</b>	
		<b>IO</b>				<b>0.1</b>	<b>0.1</b>	<b>0.1</b>	<b>&lt;0.1</b>	<b>&lt;0.1</b>	<b>0.7</b>	<b>&lt;0.1</b>	-	-	<b>&lt;0.1</b>	<b>&lt;0.1</b>	-	<b>0.1</b>	<b>&lt;0.1</b>	<b>&lt;0.1</b>	-			

Table 3.2 continued

	guild	species	n	TL (cm)	x prey	VI (%)	amp.	bif.	bip.	cal.	clu.	cra.	cte.	cyp.	ens.	fis.	har.	ido.	mys.	ner.	pol.	zoe.	oth.
Fall	HAR	<i>P. microps</i>	29	4.1±0.6	3.2	3.3	1.2	-	-	0.3	-	13.2	-	5.6	-	<0.1	62.7	-	-	3.5	1.1	-	12.4
		<b>IO</b>					<b>0.1</b>	-	-	<b>&lt;0.1</b>	-	<b>0.2</b>	-	<b>0.4</b>	-	<b>&lt;0.1</b>	<b>0.8</b>	-	-	<b>0.1</b>	<b>&lt;0.1</b>	-	-
	MYS	<i>P. platessa</i> S	4	7.8±0.8	1.5	71.4	-	-	-	-	-	-	-	2.3	25	-	-	50	-	-	2.3	-	20.5
		<b>IO</b>					-	-	-	-	-	-	-	<b>0.3</b>	<b>0.3</b>	-	-	-	<b>0.5</b>	-	<b>0.3</b>	-	-
	CAL	<i>A. tobianus</i>	5	10.7±1.3	2	80.8	-	-	-	44.6	-	-	-	25	-	-	-	-	20.2	-	-	-	10.2
		<i>C. harengus</i>	28	8.6±0.3	3.6	3.4	1.2	-	-	84	-	0.4	-	0.5	-	-	8.4	-	0.6	-	-	-	4.8
		<i>G. aculeatus</i>	8	5.4±1.2	4	57.9	15	-	-	31.3	-	-	-	0.4	-	-	11	-	2.6	-	0.1	0.5	39.2
	CAL	<i>S. sprattus</i>	30	7.5±0.7	4.5	0	0.1	-	-	71.3	-	-	-	1	-	-	20	-	<0.1	-	-	-	7.6
		<i>S. rostellatus</i>	20	11.2±1.7	2.8	26.7	6.6	-	-	51.5	-	4.2	-	13.4	-	-	7.7	-	6.5	-	-	-	10.1
		<b>x</b>			<b>3.4</b>	<b>33.8</b>	<b>4.6</b>	-	-	<b>56.5</b>	-	<b>0.9</b>	-	<b>8.1</b>	-	-	<b>9.4</b>	-	<b>6</b>	-	<b>&lt;0.1</b>	<b>0.1</b>	<b>14.4</b>
		<b>IO</b>					<b>0.1</b>	-	-	<b>0.8</b>	-	<b>&lt;0.1</b>	-	<b>0.3</b>	-	-	<b>0.3</b>	-	<b>0.2</b>	-	<b>&lt;0.1</b>	<b>0.1</b>	-
	CYP	<i>A. presbyter</i>	10	7.5±0.5	7.4	0	0.1	-	-	1.4	-	-	-	48.7	-	-	14.9	-	-	-	-	<0.1	34.8
		<b>IO</b>					<b>0.3</b>	-	-	<b>0.9</b>	-	-	-	<b>1</b>	-	-	<b>1</b>	-	-	-	-	<b>0.2</b>	-
	CTE	<i>C. lumpus</i> L	5	8.5±2.6	2.4	0	-	-	-	-	-	-	81.2	-	-	-	-	15.8	-	-	-	-	3.1
		<b>IO</b>					-	-	-	-	-	-	<b>1</b>	-	-	-	-	<b>1</b>	-	-	-	-	-
	IDO	<i>C. lumpus</i> S	5	4.9±0.6	2.4	0	5	-	-	-	-	-	-	-	-	-	-	60.3	-	-	-	-	34.7
		<b>IO</b>					<b>0.2</b>	-	-	-	-	-	-	-	-	-	-	<b>1</b>	-	-	-	-	-
Winter	CRA	<i>A. cataphractus</i>	22	12.0±1.6	1.5	8.3	0.6	-	-	-	-	91.2	-	-	-	-	-	-	2.7	-	1.6	-	3.7
		<i>M. scorpius</i> L	20	11.7±1.2	1.9	20	-	1.7	-	-	-	56.1	-	-	1.3	0.5	-	-	3.5	1	2.9	-	33
		<i>O. eperlanus</i> L	16	10.6±0.9	1.5	5.6	6.7	-	-	-	-	73.4	-	-	-	-	-	-	7.9	-	-	-	12
		<b>x</b>			<b>1.6</b>	<b>11.3</b>	<b>2.5</b>	<b>0.6</b>	-	-	-	<b>73.6</b>	-	-	<b>0.4</b>	<b>0.2</b>	-	-	<b>4.7</b>	<b>0.3</b>	<b>1.5</b>	-	<b>16.3</b>
		<b>IO</b>					<b>0.1</b>	<b>&lt;0.1</b>	-	-	-	<b>0.9</b>	-	-	<b>&lt;0.1</b>	<b>&lt;0.1</b>	-	-	<b>0.1</b>	<b>&lt;0.1</b>	<b>0.1</b>	-	-
	HAR	<i>P. microps</i>	12	3.5±0.7	1.8	33.3	10.7	-	-	8.7	-	16.7	-	-	-	-	43.3	-	-	2.1	4.2	-	14.4
		<b>IO</b>					<b>0.2</b>	-	-	<b>0.1</b>	-	<b>0.2</b>	-	-	-	-	<b>0.6</b>	-	-	<b>0.1</b>	<b>0.1</b>	-	-
	AMP	<i>Z. viviparus</i>	21	13.5±2.5	2.8	10.5	31.2	11.1	-	-	-	-	-	-	-	-	11.9	-	-	-	0.6	-	45.2
		<b>IO</b>					<b>0.6</b>	<b>0.1</b>	-	-	-	-	-	-	-	-	<b>0.4</b>	-	-	-	<b>0.1</b>	-	-
	BIF	<i>P. platessa</i> L	4	11.1±1.8	1	50	-	100	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		<b>IO</b>					-	<b>1</b>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	NER	<i>L. limanda</i> L	9	21.1±3.5	1.3	0	-	11.1	-	-	-	-	-	-	11.1	-	-	-	5.6	35.2	5.6	-	31.5
		<b>IO</b>					-	<b>0.1</b>	-	-	-	-	-	-	<b>0.1</b>	-	-	-	<b>0.1</b>	<b>0.4</b>	<b>0.1</b>	-	-
	POL	<i>L. limanda</i> S	4	9.2±1.8	1.3	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	33.3	-	66.7
		<b>IO</b>					-	-	-	-	-	-	-	-	-	-	-	-	-	-	<b>0.5</b>	-	-
	CAL	<i>C. harengus</i>	28	8.8±1.1	2.2	6.7	-	-	-	83.1	-	1.8	-	-	-	-	-	-	3.4	-	0.2	-	11.4
		<i>G. aculeatus</i>	5	5.7±1.1	1.4	61.5	-	-	-	58.8	-	-	-	-	-	-	1.2	-	-	-	-	-	40
		<i>O. eperlanus</i> S	10	7.8±1.2	1.8	16.7	-	-	-	59.1	-	11.4	0.4	-	-	-	-	-	18.3	-	5	-	5.8
		<i>S. sprattus</i>	25	6.4±0.3	1.7	6.9	-	-	-	95.9	-	-	-	-	-	-	-	-	4	-	-	-	<0.1
		<b>x</b>			<b>1.8</b>	<b>22.9</b>	-	-	-	<b>74.2</b>	-	<b>3.3</b>	<b>0.1</b>	-	-	-	-	-	<b>6.4</b>	-	<b>1.3</b>	-	<b>14.3</b>
		<b>IO</b>					-	-	-	<b>0.8</b>	-	<b>0.1</b>	<b>&lt;0.1</b>	-	-	-	-	<b>0.1</b>	-	<b>0.1</b>	-	<b>&lt;0.1</b>	-

### 3.3.3. Guild structure

Fifteen different guilds could be separated at a critical similarity value of 0.50. Seven feeding guilds were present in fall and winter, as well as eight and six in spring and summer, respectively (Fig. 3.3). While 5 guilds were represented by a single species in spring, fall and winter, only two of the 6 guilds were limited to one member in summer (Table 3.2). Results from the SIMPER analysis are shown in Figure 3.4.

Only two guilds were present year round. These two guilds were composed of fish feeding primarily on *C. crangon* or calanoid copepods (Table 3.2). The *C. crangon* eating guild (CRA) contained 19 components of mostly demersal and benthic fish. With the exception of small *Osmerus eperlanus* in the fall and small *Myoxocephalus scorpius* in summer, predominantly large size classes of fish formed CRA. Fish feeding on calanoid copepods were mostly pelagic. Within the 23 components of the calanoid copepod eating guild (CAL) there was a subgroup of fish with high resemblance (>0.9) feeding on high percentages of calanoid copepods (Fig. 3.3, Table 3.2). This subgroup comprised mainly *A. tobianus*, *C. harengus*, *S. rostellatus* and *S. sprattus* in the different seasons. Small individuals of *Hyperoplus lanceolatus*, *Merlangius merlangus* and *O. eperlanus* fed on calanoid copepods but larger individuals switched to other guilds.

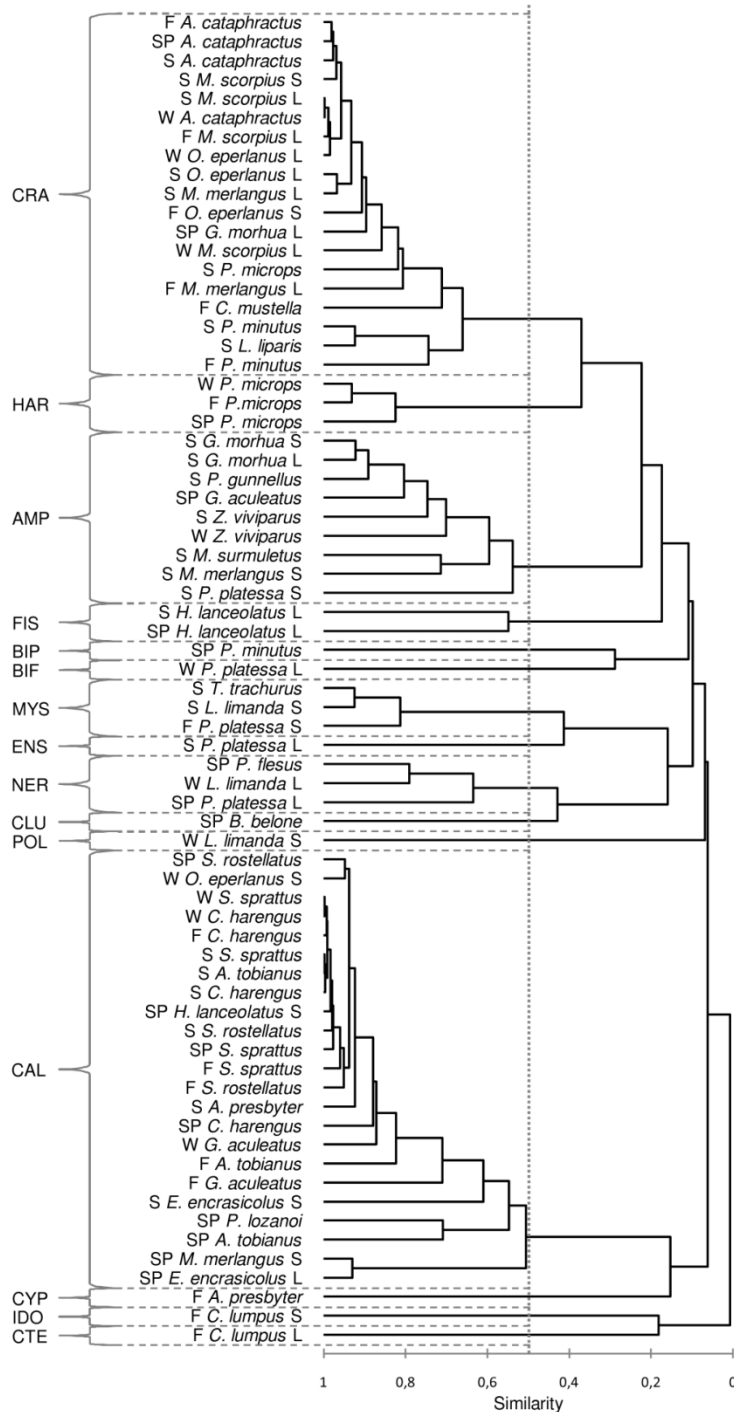


Fig. 3.3 UPGMA clustering of diet similarities for fish species of the Sylt-Rømø Bight. Dashed line indicates significant ( $p < 0.05$ ) trophic guilds identified with the bootstrapping method of Jaksic and Medel (1990). Capitals preceding species names indicate seasons: SP – spring, S – summer, F – fall, W – winter. Where applicable, size is indicated by capitals succeeding species names: L – large, S – small. AMP – Amphipoda eater, BIF – Bivalvia siphon eater, BIP – Bivalvia eater, CAL – Calanoid copepod eater, CLU – Clupeidae eater, CRA – *Crangon crangon* eater, CTE – Ctenophora eater, CYP – Cypris eater, ENS – *Ensis sp.* eater, FIS – Fish eater, HAR – Harpacticoid copepod eater, IDO – Idotea eater, MYS – Mysidacea eater, NER – Nerididae eater, POL – Polychaeta eater. Full notations of scientific names are given in Table 3.1.

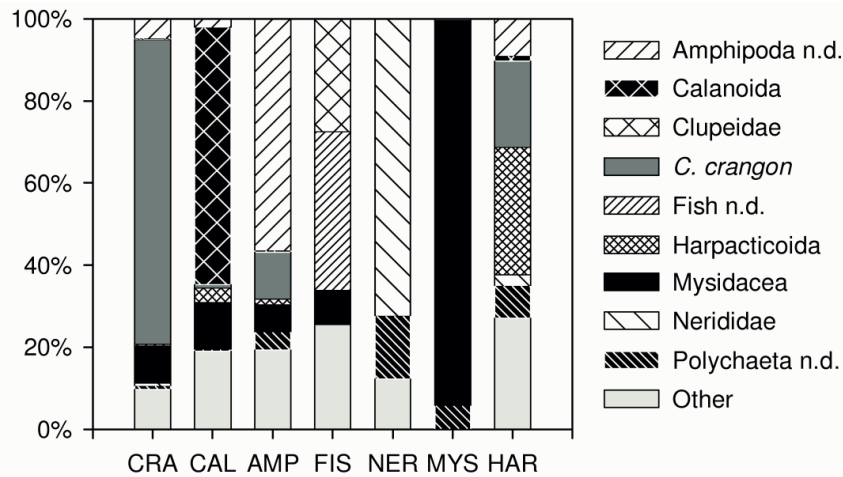


Fig. 3.4 The 9 food types contributing most to the formation of trophic guilds with more than one member. Results obtained by similarity percentage analysis (SIMPER).

The amphipod eating guild (AMP) comprised 9 components and was the second largest guild in summer, represented by 7 members. Small *M. merlangus* changed guilds from spring to summer (Fig. 3.5), although it should be noted that individuals in summer were larger (Table 3.1). Amphipods were fed on in spring by *G. aculeatus* and in winter by *Z. viviparus*. Harpacticoid copepod eaters (HAR), Mysidacea eaters (MYS) and Neredidae eaters (NER) were represented by 3 members each. HAR comprised *P. microps* in spring, fall and winter. MYS contained *Limanda limanda* and *Trachurus trachurus* in summer and *Pleuronectes platessa* in fall. NER contributors were the three flatfish species *L. limanda* in winter and *Platichthys flesus* and *P. platessa* in spring. Large *Hyperoplus lanceolatus* were piscivorous (FIS) and preyed upon Clupeidae, Ammodytidae and other fish (Table 3.2, Fig. 3.3). Eight guilds contained only a single species/season combination. These were either species only present in a specific season and specialized on specific prey, or species which switched guilds from one season to another (Fig. 3.5). Large *P. platessa* formed two guilds feeding on bivalves. One guild in spring included small *Ensis sp.* as prey (ENS) and the other fed on the siphons of larger bivalves (BIF) in winter. Thus, the different season/size combinations of *P. platessa* are all present in different guilds (Fig. 3.3). The same is true for *L. limanda*, where small individuals fed on polychaetes in winter (POL). *Belone belone* formed the second piscivorous guild (CLU), but fed at higher percentages on Clupeidae than *H. lanceolatus* and additionally included neridid polychaetes as prey (Table 3.2). *Atherina presbyter* switched to a cypris dominated nutrition in fall (CYP) and in spring *P. minutus* was the only member of a guild feeding on diverse food items with parts of bivalves

dominating (BIP). *Cyclopterus lumpus* showed the lowest similarity to the other species. Small individuals formed a guild feeding on isopods (IDO) and began feeding on ctenophores (CTE) as they grew larger.

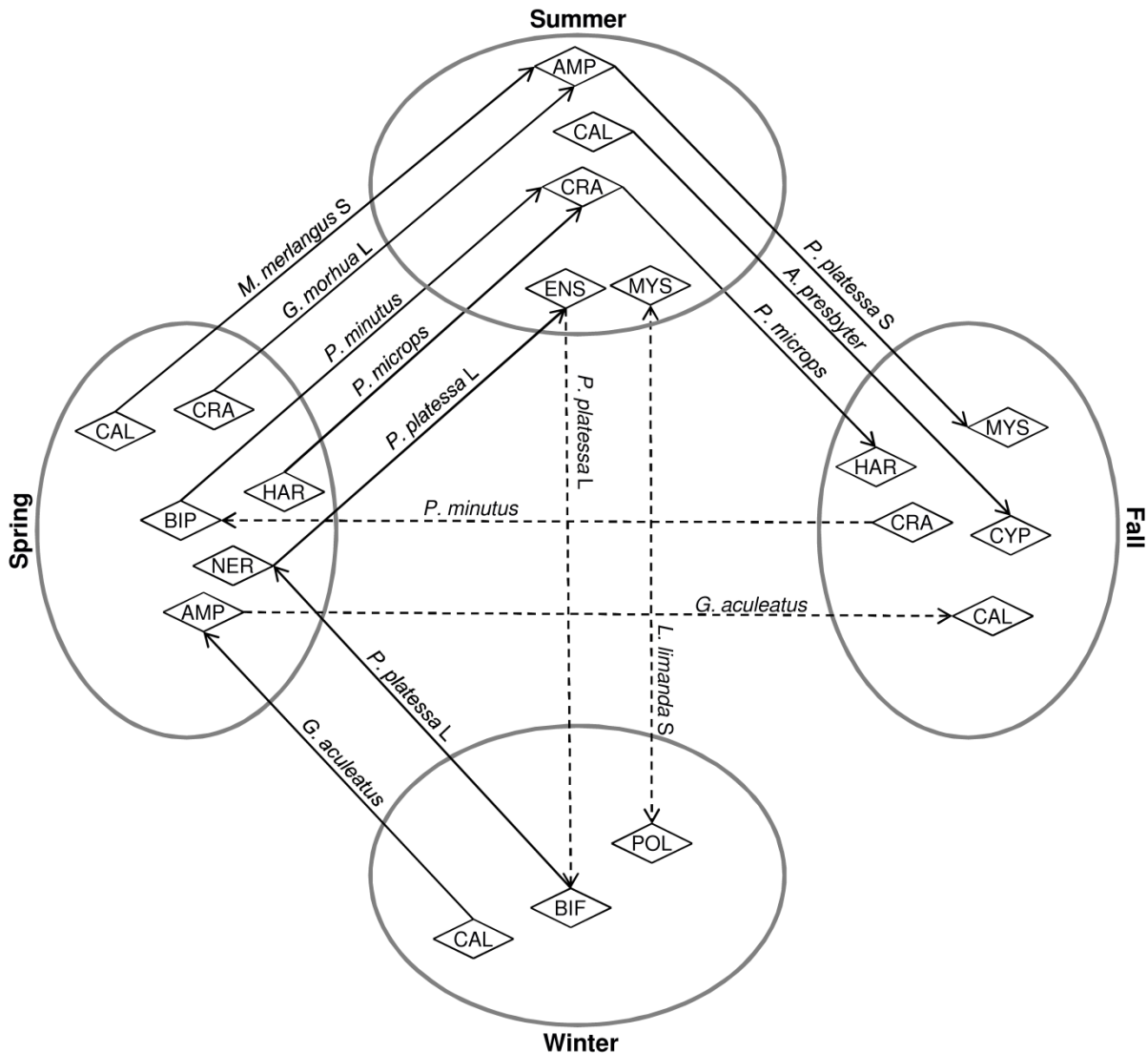


Fig. 3.5. Schematic diagram representing fish species that change guilds between seasons. Broken line indicates when the species does not occur in skipped season. Where applicable, size is indicated by capitals succeeding species names: L – large, S – small. Full notations of scientific names are given in Table 3.1.

Moving from species abundance to guild abundance, CAL was by far the most dominant guild in bottom trawl catches year round, reaching its maximum of 796.9 individuals 1000 m<sup>-2</sup> in spring and its minimum of 44.8 individuals 1000 m<sup>-2</sup> in fall (Fig. 3.6A). CRA was



present in low abundances year round, only exceeding 1 individual 1000m<sup>-2</sup> in summer and fall. The abundances of other guilds ranged from 4.1 for AMP in summer to 0.005 individuals 1000 m<sup>-2</sup> for CTE in fall. CRA and the guilds other than CAL were more important in beach seine catches than in bottom trawl catches (Fig. 3.6B). CRA dominated catches through their high abundance in summer, while HAR dominated in spring, winter and fall. The switch in diet of *P. microps* and the high abundance of this species in fall (954.3 individuals 1000 m<sup>-2</sup>) led to the decline of CRA. High abundance of HAR in winter was again caused by the high abundance of *P. microps*.

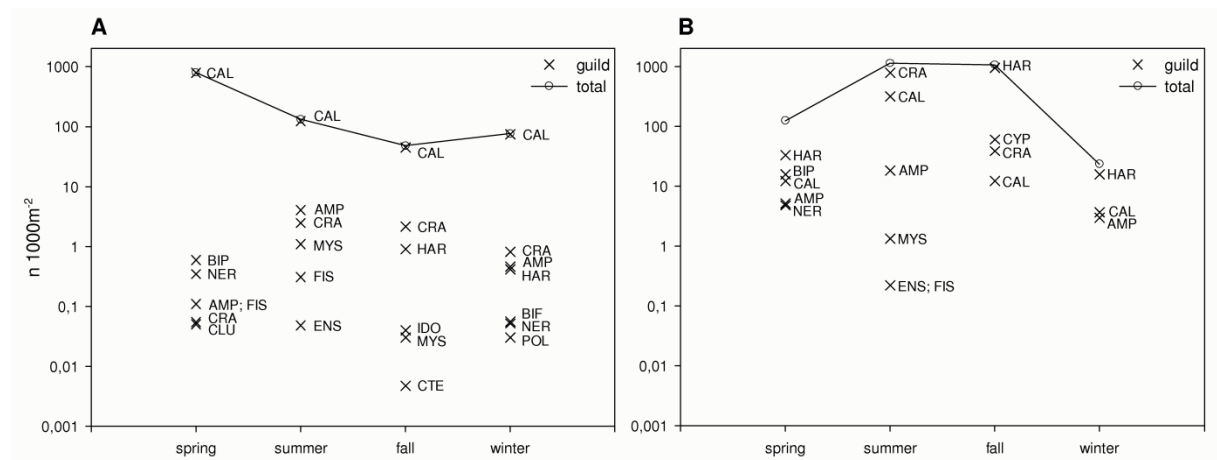


Fig. 3.6 Seasonal fish abundance shown as total abundance and per guild abundance in (A) bottom trawl catches and (B) beach seine catches. Note logarithmic axis.

### 3.4. Discussion

#### 3.4.1. Abundance and species composition

The clear dominance of juvenile and small sized fish species in the sampled area is in accordance with previous studies (Herrmann et al., 1998a; Lozán et al., 1994). Blaber and Blaber (1980) assumed that juvenile and small sized fish species use the productive shallow areas for feeding and avoidance of predators. Therefore, this study points on the function of the Wadden Sea as a nursery area for fish. However, the sampling techniques used may underestimate the importance of larger fish species, hence other more appropriate fishing techniques should be used to quantify those.

Clear changes in community structure between seasons were demonstrated, revealing migration as an important factor. Warmer temperatures during summer led to immigration of Lusitanian species like anchovy, sand smelt and striped red mullet. Also, *Scomber scombrus* and *C. labrosus* were observed, but were not present in catches or were omitted from analysis due to low sample size. For these fast swimming species the chosen sampling methods were most likely not appropriate. Furthermore, *S. scombrus* is more abundant in the adjacent North Sea (Kellnreitner and Pockberger, unpublished results). In winter, cold water temperatures led to emigration of fish into deeper zones of the North Sea, which are more stable in temperature during winter. Very few fish species, such as *P. microps*, use the bight over their entire life span.

Only *C. harengus*, *P. microps*, *A. tobianus* and *P. minutus* were dominant in abundance. Similar results were found by Herrmann et al. (1998a), although *A. tobianus* was less abundant in their samples. *C. harengus* and *P. microps* were reported as dominant in the same habitats as found in our study, but abundances were an order of magnitude lower for *C. harengus*, and even two orders of magnitude lower for *P. microps* (Herrmann et al., 1998a). *M. merlangius* also was found in higher abundances than that of our sampling. These species are known to have large interannual variations depending on multiple factors (Tulp et al., 2008). Another reason could be the sampling methods as Herrmann et al. (1998a) used a bottom trawl with a larger mesh size in the cod end (10 mm) and a push net for the shallow areas, whereas we used a beach seine. We encountered low abundances of flatfish (*L. limanda*, *P. flesus*, *P. platessa* and *S. solea*) compared to other parts of the Wadden Sea. This is in accordance with Herrmann et al. (1998c) who argued that the low number of flatfish might depend on the lower proportion of intertidal areas in the Sylt-Rømø Bight compared to other tidal basins of the Wadden Sea and the comparatively large distance to the spawning areas. *Ammodytes marinus*, *Buglossidium luteum*, *Microstomus kitt*, *Syngnatus acus* and *Trisopterus luscus* were found year round or nearly year round by Herrmann et al. (1998a), but were absent in our catches.

Estimates of gear efficiency were not included in calculations. Therefore, comparisons between the two sampling strategies have to be treated carefully, because both gears underestimate abundances, the bottom trawl more than the beach seine. The identification of seasonal differences within sampling series was not affected by this problem.

### 3.4.2. Feeding ecology and guild structure

The feeding guild system of the fish of the Sylt-Rømø Bight is characterized by a strong variation of guilds occurring in the different seasons. Only two of the 14 described feeding guilds were found year round. These two guilds, namely CAL and CRA, are the most speciose and together with HAR heavily influenced the two depth strata sampled with the two different methods. The shallower parts sampled with a beach seine differ substantially in composition of guilds from the deeper parts sampled with a bottom trawl. While benthivore species dominated the shallower parts of the Sylt-Rømø Bight, planktivore species were most abundant in the deeper parts. Fish fed on a broad prey spectrum, but nevertheless, a few prey types were of major importance. Of the 73 food items found in gut contents of fish of the Sylt-Rømø Bight, the 15 most abundant food items contributed to more than 80% of the total amount. Furthermore, attention should be directed towards the 11 of the 27 fish species that switched guilds either during ontogenetic development or for other reasons.

While the fish species in this study are often restricted to a certain feeding mode, most of them occur in a broad geographical range and feed on a large variety of prey (Daan, 1973; Robb and Hislop, 1980; Last, 1987; Herrmann et al., 1998b; Hostens and Mees, 1999; Wennhage and Pihl, 2002; Green et al., 2009). Zooplankton as well as zoobenthos species composition in the Sylt-Rømø Bight are subject to high variation throughout the year (Asmus, 1982; Martens, 1995). Certain macrobenthos and zooplankton species reach high abundances and can contribute to a high proportion of the fauna in the bight. Considering their rather generalist mode of exploitation, it seems that most fish species adapt to abundant prey items. This becomes apparent when summer is compared to the other seasons. Most changes of feeding guilds occur between summer and other seasons (Fig. 3.5). In summer, fish formed speciose guilds, feeding on amphipods, calanoid copepods and *C. crangon* (AMP, CAL and CRA). *C. crangon* is a benthic shrimp with pelagic phases that completes its life cycle in the Wadden Sea. Highest abundances were found on tidal flats and in tidal gullies in summer (Herrmann et al., 1998a), making them an ideal prey for those fish feeding on larger zoobenthos. Maximum abundances of amphipods in summer led to the formation of AMP consisting of 7 fish species. During winter this guild was only represented by *Z. viviparus*. Calanoid copepods contribute a major part to the zooplankton in the Wadden Sea throughout the year (Martens, 1995). Highest densities are found in late spring and summer in concurrence with highest abundances of zooplanktivores. During winter the number of guild components was only half that of guild components during summer, nevertheless one guild more than in summer was identified. Five of the seven guilds were single

species guilds and the mean food overlap was lower than in summer. This indicates a convergence towards abundant prey items in summer and a divergence in winter. Fish species visiting the bight occur at the same time as their prey is available. Resident fish species switch to dominant prey in summer and tend to specialize in winter where abundance of prey organisms is generally low. Similar results were found by Reum and Essington (2008) for the temperate Puget Sound estuary.

In order to have a realistic view of diet overlap, no functional groups of prey items were constructed. Overlap values therefore indicate partitioning of resources and may reveal competition for food. Consequently, interactions within guilds are likely to be stronger than interactions between different guilds (Pianka, 1980). In a system where most fish have opportunistic tendencies, the potential for competition is highest where overlap of diets is highest. This is the case for fish in CRA and CAL, where fish fed on the same food in the same season. To quantify competition, consumption of fish and biomass of prey needs to be estimated. Abundances of prey species found in previous studies (Asmus, 1982; Martens, 1995; Herrmann et al., 1998c) show strong seasonal trends. Zooplanktivorous fish (CAL, CYP), often highly mobile species, show highest abundances during times of maximum zooplankton density, as observed by Martens (1995). During this phase, fish species with southern distributions, like *A. presbyter* and *Engraulis encrasicolus*, can be present in zooplanktivorous guilds and may become competitors for boreal and resident species. Furthermore, large amounts of the ctenophore *Mnemiopsis leidyi* were observed from late spring to fall (Kellnreitner and Pockberger, unpublished results). Known as a voracious predator on zooplankton, it may represent an even larger competitor for zooplanktivorous fish feeding guilds (Kideys, 2002).

Comparing our results with those of Herrmann et al. (1998b, c), we observed an increase in abundance of zooplanktivorous guilds (CAL, CYP) and a decline in benthivorous guilds (AMP, BIF CRA, ENS, MYS, NER, POL) in the deeper parts of the bight. This suggests an increased importance of smaller pelagic prey and lower trophic levels. Results of the study on responses to climate change in fish assemblages from Engelhard et al. (2010) corroborate our findings. They found an increase in abundance of pelagic fish and an increase of lower trophic levels and planktivory in the North Sea. For the food web of the bight, this would mean that the majority of fish in the deeper parts is dependent on allochthonous production (Baird et al., 2004). Fish in the shallow parts of the bight on the other hand depend on autochthonous production. Therefore, fish of the bight depend on varying inputs, depending on season. However, interpretation of these

results should be treated with care due to high interannual variation, and long time series data are necessary to validate them.

When comparing the diets of fish obtained in the different studies (Daan, 1973; Robb and Hislop, 1980; Last, 1987; Hamerlynck and Hostens, 1993; Elliott and Dewailly, 1995; Greenstreet et al., 1997; Herrmann et al., 1998b; Hostens and Mees, 1999), for some species, a very broad spectrum was found. During these studies, various ontogenetic stages were analyzed and local prey availability should be considered when comparing data. This is particularly true for benthic and demersal fish where abundance and composition of prey is dependent on habitat structure. For *M. merlangus*, different feeding modes and food items ranging from zooplankton to crustaceans and fish were found. In pelagic fish a higher resemblance in diet was found (Last, 1987; Elliott and Dewailly, 1995; Greenstreet et al., 1997; Herrmann et al., 1998b; Hostens and Mees, 1999). In these studies calanoid copepods were the common food source for planktivorous pelagic fish. For comparisons of different habitats, the use of feeding modes as proposed by Elliott et al. (2007) is more meaningful.

The guilds identified during the sampling period can be assigned to three of the seven feeding mode functional groups (FMFG) defined by Elliott et al. (2007) for estuarine fish assemblages. In the present study all guilds demonstrated a zooplanktivorous, zoobenthivorous or piscivorous feeding mode. Although gobies were often present in zoobenthivorous guilds, it seems more appropriate to describe them as opportunists in terms of feeding modes as they are able to use a broad variety of other food sources (del Norte-Campos and Temming, 1994; Hostens and Mees, 1999; Wennhage and Pihl, 2002). The fish of the Sylt-Rømø Bight can be assigned to five FMFGs when we include *C. labrosus*, which feeds mainly on microphytobenthos (Cardona, 2001). All FMFGs (after Elliott et al. 2007), except for general omnivorous (encompassing herbivory to a certain extent) and herbivorous were temporarily represented in the sampling area. Considering the absence of herbivorous fish in marine environments at this latitude (Floeter et al., 2005), the Sylt-Rømø Bight represents a high diversity of feeding modes within a small spatial range. Nevertheless, fish species using feeding modes different than zooplanktivory and zoobenthivory were rare and often present just for short periods of the year. The occurrence of feeding modes is in accordance with the feeding modes found for other parts of the Wadden Sea (Elliott and Dewailly, 1995; Herrmann et al., 1998b; Hostens and Mees, 1999). The difference with other areas is a higher importance of zooplanktivory in the Sylt-Rømø Bight.

### 3.5. Conclusion

The feeding guild system of fish of the Sylt-Rømø Bight is characterized by high variability both in space and time. Deep and shallow areas differ in terms of their dependence on pelagic and benthic production, and seasonal variability acts on these habitats in different ways. These findings need to be taken into account in food web modeling.

Identification of potential competitive interactions and important prey items requires a high resolution of food particles. Allocation to trophic levels can be done. When comparing system functioning of different habitats another scale needs to be chosen. Due to ever present opportunistic feeding behavior in marine fish communities and local variations in prey species composition, direct comparisons of food items or narrow feeding guilds are not useful. The use of functional feeding mode groups as proposed by Elliot et al. (2007) is encouraged.

The results obtained by this study represent the basis for comparisons of Wadden Sea fish communities with other coastal areas. Because of the importance of the Wadden Sea as a nursery area, further research should encompass potential changes in production within these areas and the consequent relevance for fish on a North Sea wide level. Identification of feeding relationships and key prey species provides important information for coastal area management and may help to explain variations of fish community structure in an area subject to constant change.

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#### 4. Trophic structure of the fish community in a boreal tidal basin, the Sylt-Rømø Bight, revealed by stable isotope analysis

Florian Kellnreitner\*, Moritz Pockberger, Ragnhild Asmus, Ulrich Struck, Harald Asmus

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##### Abstract

A stable isotope ( $\delta^{15}\text{N}$ ,  $\delta^{13}\text{C}$ ) analysis was conducted to examine the fish community of a northern Wadden Sea basin, the Sylt-Rømø Bight.  $\delta^{15}\text{N}$  was used to infer trophic structure and  $\delta^{13}\text{C}$  to trace the origin of the food of 18 fish species. A baseline, using *Ensis directus* and *Littorina littorea*, was constructed to calculate the trophic positions of fish. Benthic feeding fish had higher  $\delta^{13}\text{C}$  values and were generally enriched in  $\delta^{15}\text{N}$  compared with fish feeding in the water column. A general, although not significant, trend towards  $\delta^{15}\text{N}$  enrichment in larger fish within species was found. Large individuals of *Merlangius merlangus* were at the top of the fish food web, with a calculated trophic position of 3.84. Large *Limanda limanda* had the lowest trophic position (2.94). Comparisons with gut content data from the literature are consistent with the results from the stable isotope analysis. The latter gives additional information on the provenance of the food, the distinct trophic position of fish, and the migratory behaviour of some fish species. Many fish species use both pelagic and benthic food sources. The low average trophic position of the fish that were analysed suggests the rather immature status of the bight ecosystem.

Keywords: fish food web; feeding guilds; stable isotopes, Wadden Sea  $\delta^{15}\text{N}$ ;  $\delta^{13}\text{C}$ ; 54°52' to 55°10' N, 8°20' to 8°40' E

#### 4.1. Introduction

The Wadden Sea is known for its importance with respect to juvenile fish and small-sized fish species (Rauck and Zijlstra 1978, Zander and Hartwig 1982). Commercially important fish species of the adjacent North Sea, such as herring, plaice, and sole, use these shallow areas as nursery grounds, and various fish species visit the Wadden Sea in summer to feed (Herrmann et al. 1998, Kellnreitner et al. 2011, van Beek et al. 1989). These shallow coastal waters are subject to large fluctuations in temperature and salinity. As a result, the composition and abundance of fish species is subject to large variations throughout the seasons of a year (Herrmann et al. 1998, Kellnreitner et al. 2011) and also among different years (Herrmann et al. 1998). Such variations are also observed for many of the prey species of Wadden Sea fish (Asmus 1982, Martens 1995).

A recent publication by Kellnreitner et al. (2011) identified 15 feeding guilds of fish in the area of the Sylt-Rømø Bight during the 4 seasons of a year. Feeding guilds were identified by means of gut content analysis. Gut content analysis provides detailed information on the amount of ingested material and the species composition of prey items. Nevertheless, Pinnegar and Polunin (1999) stated that gut content analysis only offers a snapshot of the actual feeding habits. The results may be subject to high variation caused by individual feeding habits, food availability, differential prey digestibility, and other factors (Pinnegar and Polunin 1999, Polis and Strong 1996).

Over recent decades, the analysis of stable isotopes has been established as a standard method used in the research on food webs and feeding relationships in terrestrial, freshwater, and marine environments (e.g., Garcia et al. 2007, Gu et al. 1996, Kelly 2000, Peterson and Fry 1987, Post 2002). The most commonly monitored atoms are carbon and nitrogen. The average enrichment of  $^{13}\text{C}$  between a consumer and its food source is approximately 1‰ (DeNiro and Epstein 1978). Even in transfers over multiple trophic levels,  $\delta^{13}\text{C}$  in the top level is close to that of the primary producers at the base of the food web. Therefore, the  $^{13}\text{C}/^{12}\text{C}$  ratio is used to derive the origin of the food of a species (France 1995, Lugendo et al. 2006). The average enrichment of  $^{15}\text{N}$  is approximately 3.4‰ per energy transfer (Minagawa and Wada 1984), and it is used to determine the trophic position (e.g., Pasquaud et al. 2010, Post 2002). In organisms with low trophic positions, high variations in isotopic composition are often encountered (Aberle and Malzahn 2003, Cabana and Rasmussen 1996). For the calculation of higher trophic positions, a baseline with organisms of a known trophic position is established

(Post 2002). Long-lived primary consumers are often chosen for this purpose because they are less subject to these variations (Cabana and Rasmussen 1996, Post 2002).

Depending on the tissue sampled, integration times can vary from days, as for mucus or liver, to years, as for bones (Church et al. 2009, Phillips and Eldridge 2006). White muscle tissue is normally analysed for determinations of the position of fish within food webs (Cabana and Rasmussen 1994, Jennings et al. 1997, Pasquaud et al. 2008). The isotopic composition of this part of the fish body reflects the diet of the last 2 to 4 months and is less variable in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  than other tissues (Pinnegar and Polunin 1999). Perga and Gerdeaux (2005) stated that the diet during the main growth period is the prime contributor to the isotopic signal.

Most information is obtained through the combined use of gut content and stable isotope analyses, although this approach has rarely been applied to entire fish communities (Akin and Winemiller 2008, Lugendo et al. 2006, Pasquaud et al. 2010, Winemiller et al. 2007). To date, there have been few studies that have analysed the food webs of fish communities in the North Sea, and particularly in the Wadden Sea. In a study by Das et al. (2003), stable isotope ratios for 34 species of North Sea fish were analysed and supplemented with dietary data from the literature to estimate the diets of marine mammals, which were the focus of that investigation. Jennings et al. (2001, 2002) used stable isotope analysis to infer trophic positions and to determine long-term trends and the effects of size on the trophic structure of the North Sea fish community.

To the best of our knowledge, to date, no study based on stable isotope analysis has investigated the fish community in the Wadden Sea. An investigation of stable isotope composition can add information regarding the trophic structure and the origin of food to the results obtained by Kellnreitner et al. (2011) and will augment the resolution of food web studies in this region (Baird et al. 2004, Baird et al. 2007, Baird et al. submitted). In this study, we used the stable isotope ratios of  $^{13}\text{C}/^{12}\text{C}$  and  $^{15}\text{N}/^{14}\text{N}$  to determine the positions of the most important fish species in the food web of the Wadden Sea. The origin of food was examined using carbon isotopes and trophic positions were calculated using nitrogen isotope data. We compared these data with the results of diet analysis by Kellnreitner et al. (2011), obtained during the same period. The results are discussed with reference to migration, opportunistic feeding behaviour, effects of habitats, and seasonality.

## 4.2. Material and Methods

The fish caught for stable isotope analysis were obtained as part of a monthly fish survey in the Sylt-Rømø Bight, northern Wadden Sea, Germany, from April 2008 to November 2009. A bottom trawl was operated from the research catamaran, 'Mya', at 8 different locations within the bight to provide good geographical coverage of the area. Additional samples, from shallow areas, were collected with a beach seine. Detailed sampling procedures and area characteristics are described in Kellnreitner et al. (2011).

Immediately after being caught, up to 15 individuals of each fish species in the catches were frozen for later analysis of stable isotope composition. In the laboratory, the fish were thawed, the total length was measured to the nearest mm, and tissue samples were taken from the dorsal white muscle. The samples were freeze-dried, ground to a fine powder with a ball mill, weighed, and encapsulated in tin capsules. These samples were then sent to the stable isotope laboratory of the Museum für Naturkunde, Berlin, for further analysis. Samples were analysed using a THERMO/Finnigan™ MAT V isotope ratio mass spectrometer (Thermo Fisher Scientific, Inc., Waltham, MA, USA), coupled to a THERMO Flash EA® 1112 elemental analyzer (Thermo Fisher Scientific, Inc.) via a THERMO/Finnigan ConFlo III interface. The precision of isotopic analysis was generally better than 0.15‰ for both carbon and nitrogen. The results are presented in parts per thousand in the standard delta notation

$$\delta = \left( R_{\text{sample}} / R_{\text{standard}} - 1 \right) 1000$$

where  $R$  is the ratio of the heavier to the lighter isotope. The standards used were Vienna Pee Dee belemnite (VPDB) for carbon and atmospheric air (AIR) for nitrogen.

We chose benthic molluscs with known benthic and pelagic food sources to establish a study baseline. For this study, we sampled *Ensis directus* and *Littorina littorea*. Whereas *E. directus* feeds on phytoplankton (Shumway et al. 1985), *L. littorea* feeds primarily on microphytobenthos and a small amount of organisms at higher trophic positions (Baird et al. 2004). We estimated *E. directus* to be at a trophic position of 2. For *L. littorea* a trophic position of 2.13 was calculated by Baird et al. (2004). Molluscs were sampled from tidal areas close to the institute at low tide. For analysis of stable isotopes, tissue was taken from the foot. Mollusc samples were treated in the same manner as described for the fish samples.

Previous studies have found enrichment of  $\delta^{15}\text{N}$  in benthic species, as compared to pelagic species at the same trophic level (Pasquaud et al. 2010, Sherwood and Rose



2005). This enrichment is caused by a higher occurrence of recycling and remineralisation in benthic habitats compared to pelagic habitats (Hughes et al. 2000, Pasquaud et al. 2010). Moreover, pelagic organisms are usually more depleted in  $^{13}\text{C}$  than benthic organisms (France 1995). We chose a linear mixing model for the calculation of the base for each fish species and created a straight line (baseline) connecting the 2 molluscs in the  $\delta^{13}\text{C}/\delta^{15}\text{N}$  plot

$$\delta^{15}N_{ib} = m\delta^{13}C_i + c,$$

where  $\delta^{15}N_{ib}$  is the estimated trophic level 2 base  $\delta^{15}\text{N}$  value of the  $i^{\text{th}}$  organism,  $m$  is the slope,  $\delta^{13}C_i$  is the measured  $\delta^{13}\text{C}$  value of the  $i^{\text{th}}$  organism, and  $c$  is the y-coordinate intercept. For the calculation of the baseline,  $\delta^{15}\text{N}$  values for *L. littorea* were converted to trophic level 2. The trophic position of each fish species was then calculated as follows:

$$TP = ((\delta^{15}N_i - \delta^{15}N_{ib}) / 2.96) + 2,$$

where  $\delta^{15}N_i$  is the measured  $\delta^{15}\text{N}$  value of the  $i^{\text{th}}$  organism, 2.96 is the average  $\delta^{15}\text{N}$  enrichment per trophic level in fish species found by Vanderklift and Ponsard (2003), and 2 is the trophic position of the baseline organisms.

For data analysis, whenever possible, fish were separated into 2 size classes. Fish smaller than 50% of the maximal total length of all catches were classified as small (S), and the others were classified as large (L). To test for possible differences in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  between species and between the different size classes of a single species, a one-factor variance analysis (ANOVA) was performed. The Tukey-Kramer test was used for multiple comparisons of the size combinations of all species. Fish species were then grouped according to feeding guilds, as identified by Kellnreitner et al. (2011). For this approach, only fish that did not change guilds between seasons were used. Differences in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  between guilds were tested by ANOVA. Prior to the ANOVA, the Kolmogorov-Smirnov test was applied to all data to verify whether it was normally distributed. For all statistical tests,  $p < 0.05$  was considered to be significant.

### 4.3. Results

The analysis of molluscs revealed higher  $\delta^{15}\text{N}$  values for *L. littorea* ( $13.83 \pm 0.23$ ) than for *E. directus* ( $11.59 \pm 0.16$ ). *E. directus* ( $-18.74 \pm 0.19$ ) was more depleted in  $^{13}\text{C}$  than

*L. littorea* ( $-13.84 \pm 0.63$ ). The correction of the trophic level of *L. littorea* from 2.13 to 2 resulted in a  $\delta^{15}\text{N}$  value of 12.99 for the calculation of the baseline.

Table 4.1 Fish species grouped after feeding guilds found by Kellnreitner et al. (2011) with sample number (n) for stable isotope analysis, total length (TL) in cm with standard deviation (sd),  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values, the calculated  $\delta^{15}\text{N}$  base (base) of every fish species and the resulting trophic level. Means per feeding guild are shown in bold. Capitals following scientific species names indicate large (L) and small (S) size class. AMP – Amphipoda eater; BIF – Bivalvia siphon eater; BIP – Bivalvia eater; CAL – Calanoid copepod eater; CLU – Clupeidae eater; CRA – *Crangon crangon* eater; ENS – *Ensis sp.* eater; FIS – Fish eater; HAR – Harpacticoid copepod eater; MYS – Mysidacea eater; NER – Nerididae eater; POL – Polychaeta eater; n.p. – not present in Kellnreitner et al. (2011)

	feeding guild	n	TL $\pm$ sd (cm)	$\delta^{15}\text{N} \pm$ sd	$\delta^{13}\text{C} \pm$ sd	base	trophic level
<i>Pholis gunnellus</i>	AMP	8	10.44 $\pm$ 1.24	16.88 $\pm$ 0.30	-16.45 $\pm$ 0.97	12.24	3.57
<i>Zoarces viviparus</i>	AMP	16	12.49 $\pm$ 2.58	16.70 $\pm$ 0.70	-15.59 $\pm$ 0.91	12.49	3.42
<b>Mean</b>				<b>16.79</b>	<b>-16.02</b>		<b>3.49</b>
<i>Ammodytes tobianus</i>	CAL	21	12.02 $\pm$ 2.09	15.72 $\pm$ 0.51	-19.41 $\pm$ 0.81	11.40	3.46
<i>Clupea harengus</i>	CAL	38	8.58 $\pm$ 1.20	16.38 $\pm$ 0.98	-18.30 $\pm$ 1.45	11.72	3.58
<i>Hyperoplus lanceolatus</i> S	CAL	3	11.30 $\pm$ 2.50	15.09 $\pm$ 0.71	-18.74 $\pm$ 0.66	11.59	3.18
<i>Sprattus sprattus</i>	CAL	29	8.67 $\pm$ 1.88	15.74 $\pm$ 0.98	-18.13 $\pm$ 1.25	11.77	3.34
<i>Syngnathus rostellatus</i>	CAL	28	10.58 $\pm$ 2.25	16.79 $\pm$ 1.27	-17.63 $\pm$ 1.22	11.91	3.65
<b>mean <math>\pm</math> sd</b>				<b>15.94 <math>\pm</math> 0.66</b>	<b>-18.44 <math>\pm</math> 0.67</b>		<b>3.44 <math>\pm</math> 0.19</b>
<i>Belone belone</i>	CLU	7	47.67 $\pm$ 13.00	16.51 $\pm$ 0.68	-16.99 $\pm$ 0.36	12.09	3.49
<i>Agonus cataphractus</i> L	CRA	8	12.10 $\pm$ 0.49	17.44 $\pm$ 0.76	-15.33 $\pm$ 1.42	12.56	3.65
<i>Agonus cataphractus</i> S	CRA	11	6.06 $\pm$ 0.57	17.04 $\pm$ 0.94	-16.27 $\pm$ 0.80	12.30	3.60
<i>Merlangius merlangus</i> L	CRA	4	17.00 $\pm$ 1.78	18.07 $\pm$ 2.55	-15.16 $\pm$ 0.74	12.61	3.84
<i>Myoxocephalus scorpius</i> L	CRA	12	9.79 $\pm$ 1.18	17.10 $\pm$ 0.63	-15.42 $\pm$ 1.08	12.54	3.54
<i>Myoxocephalus scorpius</i> S	CRA	5	7.00 $\pm$ 0.35	16.96 $\pm$ 0.59	-16.17 $\pm$ 0.37	12.33	3.56
<i>Osmerus eperlanus</i> L	CRA	13	16.35 $\pm$ 3.14	17.47 $\pm$ 1.04	-14.89 $\pm$ 1.55	12.69	3.61
<b>mean <math>\pm</math> sd</b>				<b>17.4 <math>\pm</math> 0.40</b>	<b>-15.64 <math>\pm</math> 0.59</b>		<b>3.64 <math>\pm</math> 0.11</b>
<i>Hyperoplus lanceolatus</i> L	FIS	9	20.83 $\pm$ 3.32	16.12 $\pm$ 0.95	-18.39 $\pm$ 0.64	11.69	3.50
<i>Limanda limanda</i> L	NER	3	22.17 $\pm$ 0.76	14.87 $\pm$ 0.34	-16.95 $\pm$ 0.52	12.10	2.94
<i>Platichthys flesus</i> L	NER	4	13.13 $\pm$ 1.44	16.90 $\pm$ 0.35	-15.44 $\pm$ 1.60	12.53	3.47
<b>mean</b>				<b>15.89</b>	<b>-16.19</b>		<b>3.21</b>
<i>Gasterosteus aculeatus</i>	AMP, CAL	9	5.90 $\pm$ 0.46	16.93 $\pm$ 0.56	-18.88 $\pm$ 1.35	11.55	3.82
<i>Merlangius merlangus</i> S	AMP, CAL	22	10.42 $\pm$ 1.80	16.34 $\pm$ 1.81	-17.57 $\pm$ 1.02	11.93	3.49
<i>Pleuronectes platessa</i> S	AMP, MYS	43	6.83 $\pm$ 2.06	15.73 $\pm$ 0.77	-15.36 $\pm$ 1.59	12.55	3.07
<i>Pleuronectes platessa</i> L	BIF, ENS, NER	6	14.50 $\pm$ 3.82	16.64 $\pm$ 1.30	-15.64 $\pm$ 1.12	12.47	3.41
<i>Pomatoschistus minutus</i>	BIP, CRA	23	6.27 $\pm$ 1.10	16.22 $\pm$ 0.36	-17.02 $\pm$ 0.97	12.08	3.40
<i>Osmerus eperlanus</i> S	CAL, CRA	1	9.2	16.61	-17.45	11.96	3.57
<i>Pomatoschistus microps</i>	CRA, HAR	21	4.05 $\pm$ 0.57	17.05 $\pm$ 0.45	-14.11 $\pm$ 1.78	12.91	3.40
<i>Limanda limanda</i> S	MYS, POL	15	7.81 $\pm$ 2.07	16.89 $\pm$ 1.09	-16.94 $\pm$ 2.09	12.11	3.62
<i>Platichthys flesus</i> S	n.p.	4	5.75 $\pm$ 3.18	15.56 $\pm$ 1.06	-16.89 $\pm$ 1.46	12.12	3.16
<i>Ensis directus</i>	-	3	-	11.59 $\pm$ 0.16	-18.74 $\pm$ 0.19	-	2
<i>Littorina littorea</i>	-	3	-	13.83 $\pm$ 0.23	-13.84 $\pm$ 0.63	-	2.13

Table 4.2 Results from the Tukey-Kramer test showing significant differences in  $\delta^{13}\text{C}$  (o) and  $\delta^{15}\text{N}$  (+) between the different fish species. Grey bar give MM(L) ( $\delta^{15}\text{N}$ ) and MS(L) ( $\delta^{13}\text{C}$ ) as examples for correct reading of the table. Letters in parentheses show size class small (S) and large (L). AC – *Agonus cataphractus*, AT – *Ammodytes tobianus*, BB – *Belone belone*, CH – *Clupea harengus*, GA – *Gasterosteus aculeatus*, HL – *Hyperoplus lanceolatus*, LL – *Limanda limanda*, MM – *Merlangius merlangus*, MS – *Myoxocephalus scorpius*, OE – *Osmerus eperlanus*, PF – *Platichthys flesus*, PG – *Pholis gunnellus*, PMC – *Pomatoschistus microps*, PMN – *Pomatoschistus minutus*, PP – *Pleuronectes platessa*, SR – *Syngnathus rostellatus*, SS – *Sprattus sprattus*, ZV – *Zoarces viviparus*.

	AC (S)	AC (L)	AT	BB	CH	GA	HL (S)	HL (L)	LL (S)	LL (L)	MM (S)	MM (L)	MS (S)	MS (L)	OE (L)	PF (S)	PF (L)	PG	PMC	PMN	PP (S)	PP (L)	SR	SS	ZV	
AC (S)	-		+																		+			+		
AC (L)		-	+							+												+			+	
AT	o	o	-									+		+	+						+			+		
BB			o	-																						
CH	o	o			-																					
GA	o	o				-																				
HL (S)							-					+			+											
HL (L)		o						-																		
LL (S)			o						-													+			+	
LL (L)										-		+			+											
MM (S)		o	o								-															
MM L												-				+					+				+	
MS (S)			o		o	o		o					-													
MS (L)			o		o	o	o	o			o			-								+			+	
OE (L)			o		o	o	o	o	o		o				-						+	+			+	
PF (S)																-										
PF (L)			o		o	o		o									-									
PG			o		o	o		o										-								
PMC	o		o	o	o	o	o	o		o						o		o			-		+		+	
PMN			o		o	o		o							o					o		-				
PP (S)			o		o	o	o	o		o											o		-		+	
PP (L)			o		o	o		o															-			
SR		o	o												o					o		o		-	+	
SS	o	o											o	o	o		o		o		o	o			-	
ZV			o		o	o	o	o			o									o		o	o	o	o	-

We processed samples of 18 different fish species from the Sylt-Rømø Bight (Table 4.1). Eight species were separated into small and large size classes (Table 4.1). Considerable intraspecific variation was found in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  signals. The highest enrichment in  $^{13}\text{C}$  was found in *Pomatoschistus microps* ( $-14.11 \pm 1.78$ ) and in large *Osmerus eperlanus* ( $-14.89 \pm 1.55$ ). *Ammodytes tobianus* ( $-19.41 \pm 0.81$ ), *Gasterosteus aculeatus* ( $-18.88 \pm 1.35$ ), and small *Hyperoplus lanceolatus* ( $-18.74 \pm 0.66$ ) showed the lowest  $\delta^{13}\text{C}$  values. The highest  $\delta^{15}\text{N}$  values were found for large *Merlangius merlangus* ( $18.07 \pm 2.55$ ), followed by large *O. eperlanus* ( $17.47 \pm 1.04$ ) and large *Agonus cataphractus* ( $17.44 \pm 0.76$ ) (Table 4.1). Large *Limanda limanda* and small *H. lanceolatus*, with  $\delta^{15}\text{N}$  values of  $14.87 \pm 0.34$  and  $15.09 \pm 0.71$ , respectively, were the most depleted in  $^{15}\text{N}$  compared to the other fish species (Table 4.1).

The small size class of *O. eperlanus* was represented by only one individual, and was therefore excluded from the statistical analysis. The Kolmogorov-Smirnov test showed normal distributions for the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values from all other species/size class combinations. The subsequent one-factor ANOVA results indicated significant differences between these combinations for both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values; therefore, a Tukey-Kramer test was performed (Table 4.2). Interpretation of the results from this multi-comparison test allowed separation into a depleted and an enriched group of species for both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ . A separate group contained species with intermediate values that could not be assigned to one of the other groups (Table 4.3).

Tab. 4.3 Groups obtained by the Tukey-Kramer test ( $p < 0.05$ ). not sign. – not significant. Letters in parentheses show size class small (S) and large (L). AC – *Agonus cataphractus*, AT – *Ammodytes tobianus*, BB – *Belone belone*, CH – *Clupea harengus*, GA – *Gasterosteus aculeatus*, HL – *Hyperoplus lanceolatus*, LL – *Limanda limanda*, MM – *Merlangius merlangus*, MS – *Myoxocephalus scorpius*, OE – *Osmerus eperlanus*, PF – *Platichthys flesus*, PG – *Pholis gunnellus*, PMC – *Pomatoschistus microps*, PMN – *Pomatoschistus minutus*, PP – *Pleuronectes platessa*, SR – *Syngnathus rostellatus*, SS – *Sprattus sprattus*, ZV – *Zoarces viviparus*.

$\delta^{15}\text{N}$	$\delta^{13}\text{C}$		
	enriched	not sign.	depleted
enriched	AC(L); MM(L); MS(L); OE(L); PF(L); PMC	AC(S); LL(S); MS(S); PG	GA; SR
not sign.	ZV	BB; PP(L); PMN	CH; HL(L); MM(S)
depleted	PP(S)	LL(L); PF(S)	AT; HL(S); SS

Species significantly enriched in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , when compared to the other fish species of the bight, were *P. microps* and large size classes of *A. cataphractus*, *M. merlangus*, *Myoxocephalus scorpius*, *O. eperlanus*, and *Platichthys flesus*. *Gasterosteus aculeatus* and *Syngnathus rostellatus* were depleted in  $^{13}\text{C}$  but enriched in  $^{15}\text{N}$ . Small *Pleuronectes platessa* were enriched in  $^{13}\text{C}$  but depleted in  $^{15}\text{N}$ . *Ammodytes tobianus*, small *H. lanceolatus*, and *Sprattus sprattus* were significantly ( $p < 0.05$ ) depleted both in  $^{13}\text{C}$  and  $^{15}\text{N}$ . Species showing no significant depletion or enrichment in  $^{13}\text{C}$  or  $^{15}\text{N}$  were *Belone belone*, large *P. platessa*, and *Pomatoschistus minutus*. Significant differences in  $\delta^{13}\text{C}$  between size classes of a species were only found for *M. merlangus*. Small *M. merlangus* showed depletion in  $^{13}\text{C}$ , whereas the large size class was enriched. *Limanda limanda* and *P. flesus* showed significant differences in  $^{15}\text{N}$  values. Whereas in *L. limanda*, the large size class was depleted and the small size class was enriched, the opposite trend was observed in *P. platessa*. Although not significant in most cases, a tendency towards enrichment in  $^{13}\text{C}$  and  $^{15}\text{N}$  was observed in large size classes (Fig. 4.1).

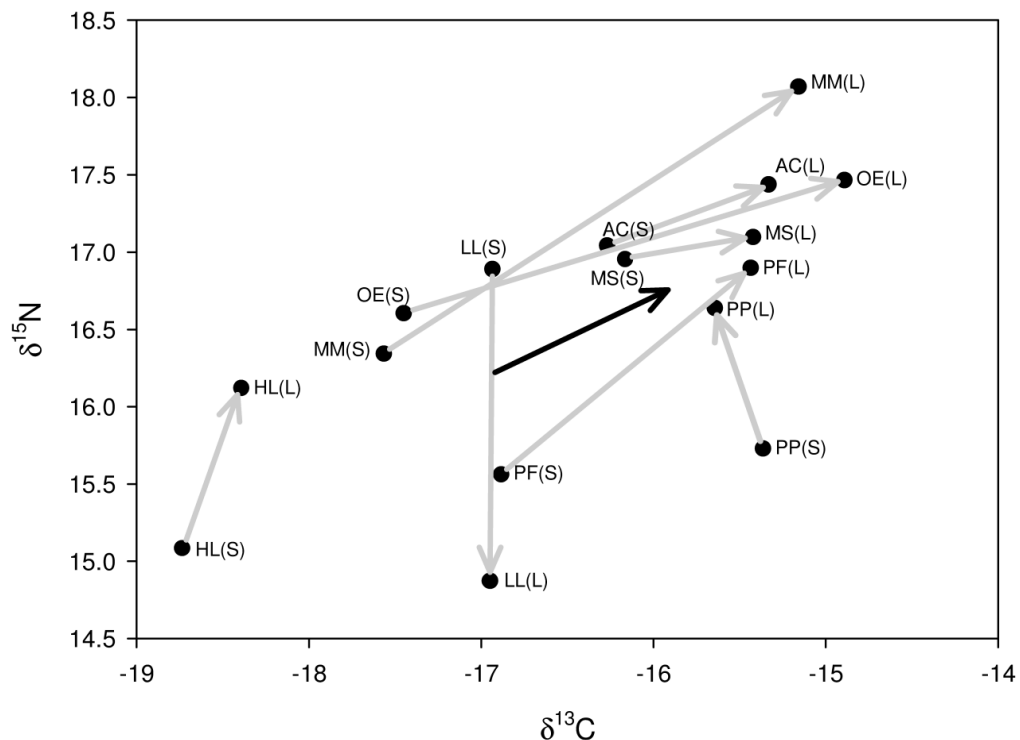


Fig. 4.1 Changes in mean  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  with changing size class (grey arrows). The black arrow represents the mean of all vectors. Letters in parentheses show size class small (S) and large (L). AC – *Agonus cataphractus*, HL – *Hyperoplus lanceolatus*, LL – *Limanda limanda*, MM – *Merlangius merlangus*, MS – *Myoxocephalus scorpius*, OE – *Osmerus eperlanus*, PF – *Platichthys flesus*, PP – *Pleuronectes platessa*.

Due to the restrictions imposed by sample size, only the 2 guilds that had the most members (CAL – Calanoid copepod eaters; CRA – *Crangon crangon* eaters) were tested for differences in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ . Significant enrichment in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  was found for CRA when compared to CAL (Fig. 4.2).

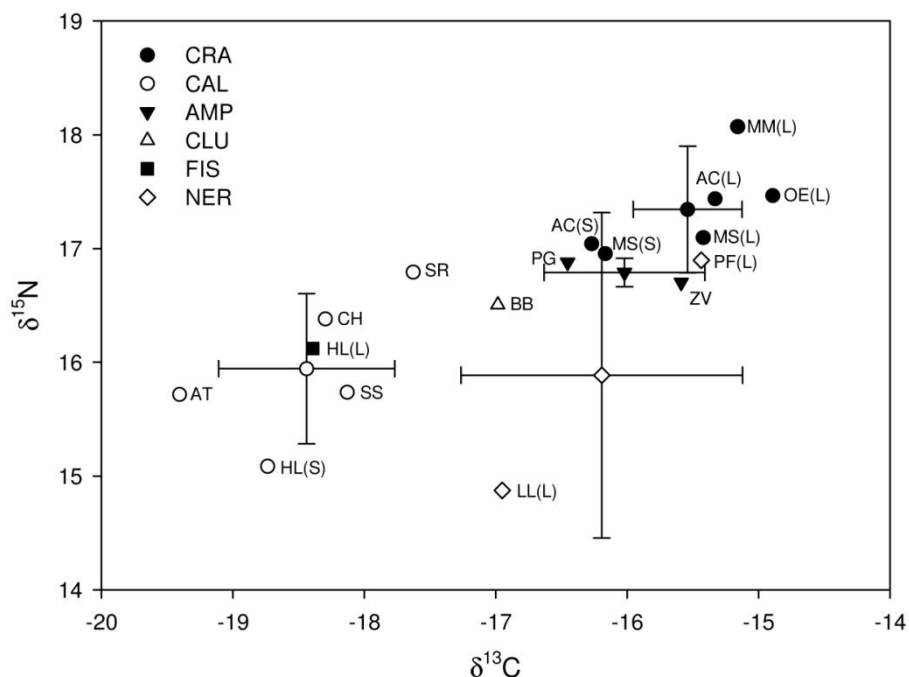


Fig. 4.2 Mean isotopic signatures ( $\delta^{15}\text{N}$ ,  $\delta^{13}\text{C}$ ) of fish grouped into feeding guilds after Kellnreitner et al. (2011). Standard deviation is only shown for guild means. Letters in parentheses show size class small (S) and large (L). AC – *Agonus cataphractus*, AT – *Ammodytes tobianus*, BB – *Belone belone*, CH – *Clupea harengus*, HL – *Hyperoplus lanceolatus*, LL – *Limanda limanda*, MM – *Merlangius merlangus*, MS – *Myoxocephalus scorpius*, OE – *Osmerus eperlanus*, PF – *Platichthys flesus*, PG – *Pholis gunnellus*, SR – *Syngnathus rostellatus*, SS – *Sprattus sprattus*, ZV – *Zoarces viviparus*.

Calculation of trophic positions with respect to the baseline yielded lower differences between species depleted and enriched in  $^{13}\text{C}$ . A higher trophic position was calculated for *A. tobianus* (3.46), although this species was depleted in  $\delta^{15}\text{N}$  by 1.33‰ when compared to *P. microps* (3.40). *Merlangius merlangus* (3.84) had the highest trophic position followed by *G. aculeatus* (3.82). Large *L. limanda* (2.94) was the only species with a trophic level lower than 3 (Fig. 4.3).

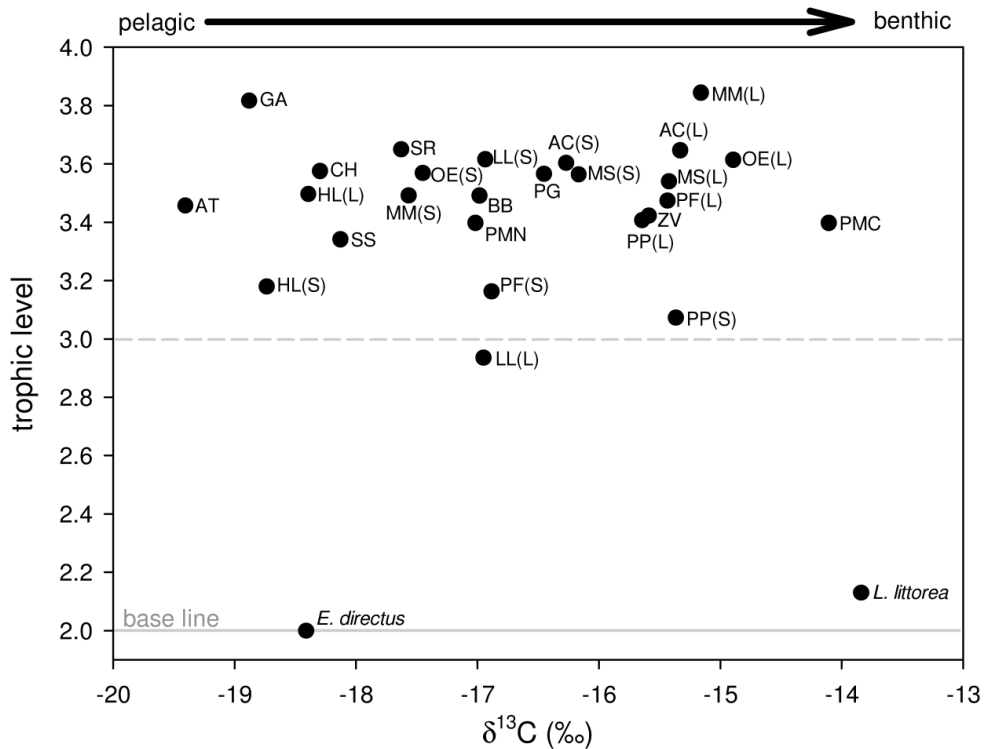


Fig. 4.3 Trophic levels of fish of the Sylt-Rømø bight calculated by creating a baseline with *Ensis directus* (*E. directus*) and *Littorina littorea* (*L. littorea*). An increase in  $\delta^{13}\text{C}$  ratio corresponds to an increasing benthic diet source. Letters in parentheses show size class small (S) and large (L). AC – *Agonus cataphractus*, AT – *Ammodytes tobianus*, BB – *Belone belone*, CH – *Clupea harengus*, GA – *Gasterosteus aculeatus*, HL – *Hyperoplus lanceolatus*, LL – *Limanda limanda*, MM – *Merlangius merlangus*, MS – *Myoxocephalus scorpius*, OE – *Osmerus eperlanus*, PF – *Platichthys flesus*, PG – *Pholis gunnellus*, PMC – *Pomatoschistus microps*, PMN – *Pomatoschistus minutus*, PP – *Pleuronectes platessa*, SR – *Syngnathus rostellatus*, SS – *Sprattus sprattus*, ZV – *Zoarces viviparus*.

#### 4.4. Discussion

The results of the stable isotope analysis of the position of Wadden Sea fish in the food web of the Sylt-Rømø Bight support the results of the gut content analysis undertaken by Kellnreitner et al. (2011) (Table 4.4). The high temporal resolution of the gut content analysis seems to overcome the potential 'snapshot' shortcoming (Pinnegar and Polunin 1999) of the method. Nevertheless, stable isotope analysis gives additional information on the provenance of the food and the distinct trophic positioning of the species. Additional assumptions on migratory behaviour can be drawn.

Tab. 4.4 Diet of fish in percent averaged over one year. Amp – Amphipods, Biv – Bivalves, Cal – Calanoid copepods, Clu – Clupeid fish, Cra – *Crangon crangon*, oFi – Other fish, Har – Harpacticoid copepods, Mys – Mysid shrimp, Pol – Polychaetes, oZo – Other zooplankton, oth – Other organic material. Letters in parentheses show size class small (S) and large (L). AC – *Agonus cataphractus*, AT – *Ammodytes tobianus*, BB – *Belone belone*, CH – *Clupea harengus*, GA – *Gasterosteus aculeatus*, HL – *Hyperoplus lanceolatus*, LL – *Limanda limanda*, MM – *Merlangius merlangus*, MS – *Myoxocephalus scorpius*, OE – *Osmerus eperlanus*, PF – *Platichthys flesus*, PG – *Pholis gunnellus*, PMC – *Pomatoschistus microps*, PMN – *Pomatoschistus minutus*, PP – *Pleuronectes platessa*, SR – *Syngnathus rostellatus*, SS – *Sprattus sprattus*, ZV – *Zoarcetes viviparus*. Results from Kellnreitner et al. (2011).

	N	Amp	Biv	Cal	Clu	Cra	oFi	Har	Mys	Pol	oZo	oth
AC	58	11.6	3.3	-	-	71.8	0.8	-	1.2	>0.5	1.6	9.2
AT	55	0.5	>0.5	48	-	-	1.4	3.2	13.2	7.3	22.8	3.4
BB	5	-	-	-	30	1.5	20.3	-	-	34.9	-	13.3
CH	106	0.6	>0.5	73.2	-	0.7	1.5	2.4	4.7	>0.5	12.8	3.7
GA	20	21.7	-	38.2	-	0.7	-	4.1	0.9	19	4.5	11
HL (L)	13	-	-	-	14.9	7.6	42.8	-	7.1	7.1	13.7	6.8
HL (S)	15	-	-	72.5	-	-	-	1	>0.5	-	17.1	9
LL (L)	9	-	48.1	-	-	-	-	-	5.6	40.7	-	5.6
LL (S)	13	0.6	-	-	-	-	-	-	31.3	47.3	8.3	12.5
MM (L)	25	-	22.3	-	3.2	51	3.1	-	11.3	0.8	-	8.2
MM (S)	21	16.9	-	17.7	-	6.9	-	>0.5	15.7	>0.5	34.5	7.7
MS (L)	37	-	1.3	-	-	75.4	4.9	-	1.2	3	-	14.3
MS (S)	10	15.7	-	-	-	58.3	-	-	10	-	10	6.1
OE (L)	22	5.7	-	-	1.4	68	4.9	-	10.9	2	-	7.2
OE (S)	15	9.8	2.5	32.1	-	27.7	-	-	17.8	2.5	2.7	4.9
PG	6	85.9	-	-	-	1.3	-	-	1.3	-	1.9	9.7
PF	7	-	-	-	-	14.3	-	-	-	81	-	4.8
PP (L)	12	-	66.8	-	-	-	-	-	5.6	19.1	2.9	5.7
PP (S)	26	13	17.4	-	-	6.2	-	3	27.5	16.6	2.4	14
PMC	70	5.8	>0.5	2.2	-	26.3	>0.5	32.9	2.4	7.7	16.1	6.5
PMN	74	6.5	16.2	1.6	-	15.9	1.4	5.1	9.8	2	11.1	30.3
SS	102	>0.5	>0.5	81.2	-	>0.5	>0.5	6.9	1.4	>0.5	9	1.4
SR	67	5.5	>0.5	59.4	-	1.9	>0.5	2.6	7.5	>0.5	12.9	9.9
ZV	27	42.9	15.5	-	-	-	-	7.6	-	0.7	15.8	17.4

The mixing model developed by Vander Zanden et al. (1999) for lake habitats requires the sampling of numerous primary consumers to establish a baseline. This approach demands considerable sampling effort and exceeded the aim of this study. We chose a linear mixing model, as utilised by Post (2002). Studies by Baird et al. (2004, 2007)



pointed to 2 major sources of organic matter. These 2 sources, the water column and the intertidal/benthic area, were used to explain the origin of food in this study. The results of the stable isotope analysis to describe the origin of food fit well with the results from the gut content analysis reported in Kellnreitner et al. (2011). In general, a broad range of  $\delta^{13}\text{C}$  was found for the fish species of the Sylt-Rømø Bight. Many fish species seem to obtain their carbon from both pelagic and benthic sources. The Wadden Sea carbon cycle depends, to a large degree, on phytoplankton imported into the system by the tides (Baird et al. 2004). Nevertheless, benthic interactions are important because most of the carbon is recycled there.

Considerable variation was found in both carbon and nitrogen isotopic compositions within the different fish species. Gannes et al. (1997) stated that this variation is explained by body condition, digestive traits, and dietary patterns. The highest variation in  $\delta^{15}\text{N}$  was observed for fish species that, in the study by Kellnreitner et al. (2011), showed a large food spectrum. This is not only the case for *L. limanda* and *P. platessa*, which were found in multiple guilds, but also for *M. merlangus* and *S. rostellatus*. Large *M. merlangus* were only found in CRA, but other studies showed opportunistic feeding behaviour for this species (Elliott and Dewaily 1995, Hamerlynk and Hostens 1993, Hostens and Mees 1999). The high variation in *S. rostellatus* may be attributed to restrictions in dissecting muscle tissue due to the slender form and the small size of these fish.

Fish of the CAL guild were found at a generally higher trophic position than assumed by Baird et al. (2004). The results correspond more closely with the trophic positions found by Yang (1982). Very high trophic positions, as compared to our results, were found by Christensen (1995). These differences could be attributed to differences in size; however, none of these studies gave information on the size of fish analysed. Hansson et al. (1997) attributed the higher trophic position of zooplanktivorous fish to a higher trophic position of zooplankton due to feeding on heterotrophic microorganisms.

The generally low trophic position of fish in the study area may be explained by the relatively low organisation, and thus immature status, of the Sylt-Rømø Bight (Baird et al. 2004, Neira and Arancibia 2004). This is in agreement with Odum (1969), who describes predominantly small generalists in simple and short food chains for systems in a developmental stage. Baird et al. (2004) found *M. merlangus* at the highest trophic position (3.74) in the Sylt-Rømø bight system. They pointed out that the low average trophic level is due to short carbon cycles, the high amount of imports into the bight, and the level of exports out of the system. Within the bight system, juvenile fish use the

highly abundant low trophic level food during their main growth period. Both pelagic and benthic food sources are important and only a few species use food items from one of these sources exclusively.

For several fish species, comparisons between the isotopic composition and the diet analysis data were not consistent. *Gasterosteus aculeatus* was found at a high trophic position compared to its food (Table 4.4). The proportion of amphipods and polychaetes would suggest a more benthic origin of food than that found with the analysis of carbon isotopes. *Gasterosteus aculeatus* is known to migrate between freshwater and marine habitats. Low  $\delta^{13}\text{C}$  values could point to feeding of *G. aculeatus* in a freshwater environment and a subsequent migration to the marine area. Organisms feeding in freshwater environments display lower  $\delta^{13}\text{C}$  values than organisms feeding in marine environments (Dufour and Gerdeaux 2001).

Further, the isotopic signature of *B. belone* could be influenced by migration. This species enters the bight in spring for reproduction and feeding and is present for only a short period of the year. For the rest of the year, *B. belone* is travelling long distances and feeds in the open sea, which could be reflected in isotopic composition. This could mean a higher trophic position for this species as offshore organisms seem to be depleted in  $\delta^{15}\text{N}$  compared to organisms found nearer the shore (Sherwood and Rose 2005). The consumption of polychaetes and other low trophic level prey (Table 4.4) also affects the *B. belone*  $\delta^{15}\text{N}$  values, which would be higher with the exclusive fish diet that is generally assumed for this fish species.

Large *L. limanda* were found at a surprisingly low trophic position. It was the only species in which large individuals were significantly depleted in  $\delta^{15}\text{N}$  in comparison to small individuals. This may result from the high proportion of mussels in the diet of large *L. limanda* (Table 4.4). Small *L. limanda* prey on a higher proportion of small crustaceans, and might therefore have a higher trophic level. Jennings et al. (2002) found a similar depletion in large *P. platessa*, compared to small ones, and came to the same conclusion.

*Pomatoschistus microps* had the highest  $\delta^{13}\text{C}$  values, which can be attributed to the high amount of harpacticoid copepods in their food (Table 4.4). *Pomatoschistus microps* is also the only species in this area feeding mainly in the intertidal areas (Kellnreitner et al. 2011). Pockberger et al. (submitted) found that the microphytobenthos, which is enriched in  $\delta^{13}\text{C}$  as compared to phytoplankton (Riera et al. 1996), is an important source of the food for *P. microps*.

Stable isotope analysis gives information on distinct trophic positions and the origin of food. Nevertheless, the importance of gut content analysis for interpretation of the results should be highlighted (Lugendo et al. 2006, Pasquaud et al. 2010). A lack of consistency between gut content results and stable isotope analysis might indicate migratory behaviour, specific digestive traits, or point to overlooked food sources. Only a combination of both methods gives a good assessment concerning the food sources of fish, particularly in highly variable environments such as the Wadden Sea.

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## 5. Feeding interactions between the introduced ctenophore *Mnemiopsis leidyi* and juvenile herring *Clupea harengus* in the Wadden Sea.

Florian Kellnreitner, Moritz Pockberger, Ragnhild Asmus, Harald Asmus

Submitted to *Biological Invasions*.

### Abstract

We analysed feeding interactions between *Mnemiopsis leidyi* and juvenile herring *Clupea harengus* in the Wadden Sea. Abundance, diet overlap, prey selectivity and stable isotope composition ( $^{15}\text{N}$ ,  $^{13}\text{C}$ ) of both species were assessed from June to September 2010. High abundance of *C. harengus* was found in June and July ( $2.3 \pm 1.4 \text{ ind.m}^{-3}$ ) followed by a steep decline from August to September ( $0.1 \pm 0.1 \text{ ind.m}^{-3}$ ), coinciding with a dramatic increase in *M. leidyi* abundance ( $10.3 \pm 8.2 \text{ ind.m}^{-3}$  during September). These two species showed a high overlap in their respective diets (copepods, meroplankton) during the study period. Based on stable isotope analysis *C. harengus* and *M. leidyi* were assigned to a trophic level of 3.08 and 2.47, respectively. Furthermore, we assessed the potential of competition between *M. leidyi* and *C. harengus* in a mesocosm experiment. Results indicated that intraspecific competition in *C. harengus* seemed to be greater than interspecific competition with *M. leidyi*. Due to their temporarily high diet overlap, competition between these two species could occur should their common food resource be limited. Healthy stocks of planktivorous fish might therefore increase the resistance of a system against zooplanktivorous invaders such as *M. leidyi*, which need to be taken into consideration in fisheries management decisions.

*Keywords:* *Mnemiopsis leidyi*; *Clupea harengus*; food overlap; competition; invasive species

### 5.1. Introduction

The increase of abundances of jellyfish in marine ecosystems all over the world is currently a matter of concern (Attrill et al. 2007; Lynam et al. 2006; Pauly et al. 2009; Richardson et al. 2009) and there have been numerous discussions on the causes and consequences of jellyfish blooms (Bilio and Niermann 2004; Oguz et al. 2008; Parsons and Lalli 2002; Purcell 2005; Purcell et al. 2007).

Since the introduction of *Mnemiopsis leidyi* A. Agassiz 1865 into the Black Sea and consequent mass occurrences in the late 1980s, this ctenophore has been the focus of many studies (e.g. Bilio and Niermann 2004; Gucu 2002; Purcell et al. 2001; Shiganova 1998; Vinogradov et al. 1996). Originating from the east coast of America, it was introduced in the 1980s via ballast water of cargo ships into the Black Sea, where it established in a short period of time (Kideys 2002; Shiganova 1998). In the following two decades *M. leidyi* spread to the Seas of Azov, Marmara and eastern Mediterranean and was introduced to the Caspian Sea (Purcell et al., 2001). A second introduction from New England to the Baltic and North Sea took place around 2005 (Reusch et al. 2010). Almost simultaneous reports from the Baltic Sea (Javidpour et al. 2006), North Sea (Boersma et al. 2007), Wadden Sea (Faasse and Bayha 2006) and Skagerrak and Kattegat (Hansson 2006; Oliveira 2007; Tendal et al. 2007) indicate that this invasion may have been unrecognized for several years (Faasse and Bayha 2006).

The consequences for the ecosystems invaded by *M. leidyi* have been controversially discussed. This jellyfish is held responsible for diminishing zooplankton abundance and diversity in invaded habitats (Riisgård et al. 2011; Roohi et al. 2008; Shiganova 1998). *M. leidyi* can have an augmenting effect on phytoplankton abundance by grazing on zooplankton in its native habitats (Deason and Smayda 1982) and may exert similar influence in invaded habitats (Riisgård et al. 2007, Shiganova et al. 2004a, b). An important part of research concentrates on detrimental effects of *M. leidyi* on fish populations. After a massive bloom in the Black Sea in 1989 *M. leidyi* was held responsible for the coinciding collapse of pelagic fish populations by predation on eggs and larvae and competition for zooplankton food (Shiganova et al. 2001; Shiganova and Bulgakova 2000; Vinogradov et al. 1996). Vinogradov et al. (1996) calculated the amount of zooplankton consumed by *M. leidyi* and the most important zooplanktivorous fish stocks. They concluded that *M. leidyi* consumed large amounts of the zooplankton biomass and that together with fish, it is likely that they consume the complete daily zooplankton production. They hypothesized the collapse of the fish stock as a result of the competition between fish and the ctenophores. These hypotheses have been

controversially discussed and more recent publications state that it is overfishing and a regime shift in the 1980s what played a prominent role in this decay (Bilio and Niermann 2004; Gucu 2002).

There is general consensus about the need for considerable research effort to predict the possible impact of *M. leidyi* on the ecosystems of the North and Baltic Sea (Boersma et al. 2007; Hansson 2006; Javidpour et al. 2006). In fact, several studies have assessed interactions that *M. leidyi* may have with indigenous species. Riisgård et al. (2007) found even higher densities of *M. leidyi* than those observed in the Black Sea in Limfjorden (Denmark) and estimated that *M. leidyi* filtered copepods from up to 80% of the water column. Javidpour et al. (2009 a, b) studied the population dynamics and predation of *M. leidyi* in Kiel Bight (Baltic Sea). Small size classes of *M. leidyi* dominated the population in abundance, and under favourable conditions the population doubled its size in a few days. No time overlaps with peaks of ichthyoplankton were observed. Some studies have focussed on the effect that the invasive species might have on cod stocks in the Baltic Sea. Haslob et al. (2007) found spatial and temporal overlap of *M. leidyi* with cod eggs but Jaspers et al. (2011) found selection of *M. leidyi* against cod eggs. In the North Sea Hamer et al. (2010) found no substantial spatial overlap of *M. leidyi* with fish eggs and stable isotope analysis revealed other food items as main prey. They supposed that competition of *M. leidyi* with zooplanktivorous fish for food is more likely, but so far this has remained unexplored.

This investigation was based on diet analyses of introduced *M. leidyi* and *Clupea harengus*, a native zooplanktivorous fish species. We measured diet overlaps, prey selectivity, stable isotope signature and abundance of both species and tested the potential for competition in a mesocosm experiment. We hypothesize significant food overlap of *M. leidyi* with zooplanktivorous fish in the Wadden Sea area and therefore a potential for competition for common resources. To our knowledge this is the first study calculating diet overlap of *M. leidyi* and fish carried out on individuals caught at the same time and location.

## 5.2. Material and Methods

### 5.2.1. Sampling

Sampling was done monthly from 14 June 2010 to 14 September 2010 within the area of the Sylt-Rømø Bight ( $54^{\circ} 52'$  to  $55^{\circ} 10'$  N,  $8^{\circ} 20'$  to  $8^{\circ} 40'$  E, Fig. 5.1). The bight is located in the most northern part of the German Wadden Sea, which is divided into a Danish and a German part. Six stations were selected in the German part of the bight, representing deeper (5-10 m; stations 2, 4, 6), shallower (2-4 m; stations 1, 3, 5), exposed and sheltered parts (Fig. 5.1). Samples were taken during daylight hours around low tide. Sampling of *C. harengus*, *M. leidy* and zooplankton was carried out within a maximum of 1 hour per station.

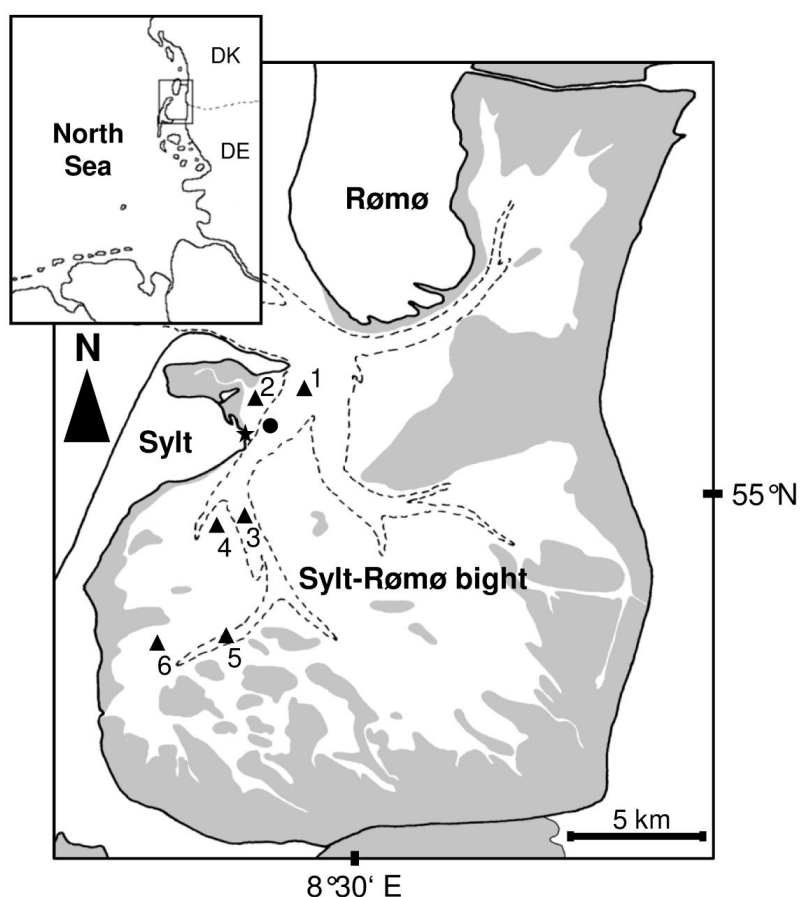


Fig. 5.1 Location of the sampling stations (triangles) within the area of the Sylt-Rømø Bight. The star indicates sampling location (near the AWI-institute) of *C. harengus* and *M. leidy* for stable isotope analysis and the experiment. The circle indicates sampling location (Lister Ley) of zooplankton for the experiments. Tidal gullies are represented by dashed line and tidal flats by grey areas.

*C. harengus* was caught with a bottom trawl (mouth opening 21 m<sup>2</sup>, 32 to 16 mm mesh net with 6 mm mesh net in the cod end) towed for 15 minutes at a speed of 2 knots. At each station 1 benthic haul was done, except for the deeper stations, where an additional pelagic haul was taken. *C. harengus* was counted and measured to the nearest 0.5 cm (total length). A subsample was taken whenever big catches were present. At each station 5 specimens were fixed in 5% buffered formalin-seawater solution for gut analysis. Prior to analysis *C. harengus* was soaked in freshwater for at least 12 hours to prevent working with formalin samples. Individuals were weighed to the nearest 0.01 g, measured to the nearest mm and dissected. Stomach contents were identified to the highest taxonomic separation possible.

*M. leidyi* were sampled with a CalCOFI net (1 m opening and 500 µm mesh net). At each station 3 replicate vertical tows from the bottom to the surface were taken. *M. leidyi* were counted and lobate length (from statocyst to end of lobe) measured to the nearest 0.5 cm. Individuals less than 3 cm were summed up in a single size class. Aboral (from statocyst to mouth) and lobate length (Mutlu 1999) of a subsample of 5 specimens per station were measured to the nearest mm. The individuals of this subsample were fixed in 5% buffered formalin-seawater solution in separate containers immediately after catching and measuring for later analysis of diet. In the laboratory *M. leidyi* samples were rinsed through an 80 µm sieve with freshwater and all plankton were identified to the highest taxonomic separation possible.

Zooplankton was sampled with a plankton net (0.6 m opening and 200 µm mesh net). At each station a vertical tow from the bottom to the surface was performed. Samples were preserved in 5% formalin-seawater solution for later analysis.

#### 5.2.2. Abundance, diet overlap and prey selectivity

Abundance of *C. harengus* and *M. leidyi* was standardized to 1000 m<sup>-3</sup>. Overall abundances in the bight were calculated using weighted means considering the different depths of the bight by surface.

Volume of prey species in the gut contents was estimated by comparing prey organisms with three-dimensional shapes to which they most closely resemble (Hyslop 1980). Necessary dimensions were measured to the closest 0.05 mm. For abundant prey species mean volumes based on the measurement of ten individuals were taken. Diet overlaps were calculated with mean values of volumetric index per species per prey after Pianka's (1973) niche overlap index

$$O_{jk} = O_{kj} = \frac{\sum_i^n p_{ij} p_{ik}}{\sqrt{\sum_i^n p_{ij}^2 \sum_i^n p_{ik}^2}}$$

where  $p_{ij}$  and  $p_{ik}$  are the proportions of the  $i^{\text{th}}$  prey type used by the  $j^{\text{th}}$  and the  $k^{\text{th}}$  species respectively (Pianka 1973). The index results in values between 0 and 1 (or between 0 and 100%). This signifies overlap of food resource use of two consumers from zero to complete overlap.

Intraspecific food overlap was calculated monthly by the method proposed by Wallace and Ramsey (1983) by randomly dividing the samples 30 times in two sets and calculating the diet overlap each time. High intraspecific overlap (>60%) signifies good characterisation of diets and implies good reliability of interspecific diet overlap values.

Prey selection of *C. harengus* and *M. leidyi* in the different month was assessed with the electivity index of Pearre (1982)

$$C = \left( \frac{\chi^2}{n} \right)^{\frac{1}{2}}$$

based on the  $\chi^2$  notation

$$\chi^2 = \frac{n(|a_d b_e - b_d a_e| - n/2)^2}{abde}$$

where  $a$  is the number of individuals of prey species  $a$  and  $b$  is the sum of all the other prey species except species  $a$  in the diet (subscript  $d$ ) and the environment (subscript  $e$ ) respectively.  $a = a_d + a_e$ ,  $b = b_d + b_e$ ,  $d = a_d + b_d$ ,  $e = a_e + b_e$  and  $n = a_d + a_e + b_d + b_e$ .  $C$  was calculated for the seven most abundant species found in the diets of *C. harengus* and *M. leidyi*.

### 5.2.3. Stable isotope analysis

On 4 September 2010 *C. harengus* and *M. leidyi* were collected close to the AWI-institute (Fig. 5.1) for stable isotope analysis. For *C. harengus* a portion of the left caudal muscle tissue was extracted. *M. leidyi* were starved for 2 days in a planktonkreisel (Greve 1968, Hamner 1990) with filtered seawater through flow and the whole animal was rinsed with purified water before taken for analysis. Samples were freeze dried, pulverized using a ball mill, weighed and encapsulated in tin capsules. Samples were analysed for  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  "with a THERMO/Finnigan MAT V isotope ratio mass

spectrometer, coupled to a THERMO Flash EA 1112 elemental analyzer via a THERMO/Finnigan ConFlo III- interface in the stable isotope laboratory of the Museum für Naturkunde, Berlin. Standard deviation for repeated measurements of lab standard material peptone was generally better than 0.15 per mill (‰) for nitrogen and carbon, respectively” (Mayr et al. 2010). Standards defined as zero values were Vienna Pee Dee Belemnite (VPDB) for carbon and atmospheric air (AIR) for nitrogen.  $\delta$  values are in parts per thousand and calculated by

$$\delta = \left( R_{\text{sample}} / R_{\text{standard}} - 1 \right) 1000$$

where  $R$  is the ratio of the heavy to the lighter isotope. Trophic levels ( $Tl$ ) were calculated by

$$Tl = \lambda + \left( \delta^{15}N_{\text{secondary consumer}} - \delta^{15}N_{\text{base}} \right) / \Delta_n$$

where  $\lambda$  is the trophic position of the organism used to estimate  $\delta^{15}N_{\text{base}}$  and  $\Delta_n$  is the enrichment of  $\delta^{15}N$  per trophic level. To estimate the  $\delta^{15}N_{\text{base}}$  a mussel (*Ensis americanus*) and a snail (*Crepidula fornicata*) were chosen (Post 2002). We estimated these molluscs at a trophic position of 2. Individuals of these molluscs were collected on a tidal flat close to the AWI-institute (Fig. 5.1) and tissue from the feet was extracted. Samples were then treated and analysed the same way as fish samples. Results from SI analysis were tested for significant differences with a two-sided Mann-Whitney U test ( $p < 0.05$ ).

#### 5.2.4. Experiments

A mesocosm experiment was run between 14 August 2010 and 20 September 2010. *C. harengus* and *M. leidyi* were obtained from tidal waters close to the institute (Fig. 5.1). *C. harengus* was caught using a lift net with a bucket attached in the middle to avoid contact of the fragile juveniles with the net and air. They were transferred to a 2000 L tank with through flow. *M. leidyi* was dipped from near surface with fine aquaria nets. The jellyfish were transferred to a planktonkreisel with through flow, where they were kept until the start of the experiment. The experiment was run in two sets because of limited space for tank installations. Eight cylindrical double walled black PVC tanks with a diameter of 1.9 m and a volume of 2000 L were used for the experiment. The tanks were run under through flow with filtered seawater (sandfilter and 200  $\mu\text{m}$  mesh net) at a rate of  $74 \pm 7 \text{ Lh}^{-1}$  per tank. Inflow was positioned close to the tank wall with 2 outlets in different depths to create a slow circulating water body. The outflow was filtered over a

cylinder (11 cm diameter, 40 cm high) with cut-outs covered by 200 µm mesh net to ensure slow outflow and prevent loss off *M. leidy* and zooplankton.

Prior to the experiment *C. harengus* was starved for 2 days. At the beginning of the first experimental run in August *C. harengus* and *M. leidy* were carefully transferred to the tanks in different densities (Tab. 5.1). For each treatment 2 replicates were carried out in randomly chosen tanks. *M. leidy* densities were chosen from the highest density found in the Sylt-Rømø Bight 2009 (16 individuals m<sup>-3</sup>; Fischer, 2008). After 7 days specimens of *M. leidy* were counted and missing ones replaced. Temperature and salinity were measured three times a day. Zooplankton in a natural composition was added daily to the tanks through a perforated PVC tube with a diameter of 2.5 cm to ensure evenly distribution of zooplankton in the water column. Zooplankton was caught directly before distribution to the tanks with the plankton net (0.6m diameter, 200 µm mesh net) in the Lister Ley (Fig. 5.1) with 3 horizontal hauls of 10 min each at a speed of approximately 1.5 knots. Tanks were supplied with food for 14 days. At the end of the experiment the fishes were starved for two days, anesthetised and killed with an overdose of MS 222. They were measured to the nearest mm, weighed and oven dried at 50°C until constant weight.

The second experimental set started on 3 September 2010 and was performed following the same procedure of the first one.

The ratio of dry weight to wet weight (DW/WW) was used to determine the energy density of *C. harengus*. Energy density is closely related to nutritional condition and is well suited to assess short-term changes in condition of small bodied fish (Ning et al. 2012). In a pre-experiment DW/WW was tested as an indicator for energy density for *C. harengus*. Fish were reared at 3 different zooplankton concentrations (starvation, normal density, 2.5 fold density) and wet weight and dry weight determined at the end of the pre-experiment. Significant differences (two sided Mann-Whitney U test,  $p < 0.05$ ) were found between all the different treatments, so this method was chosen for evaluation of *C. harengus* condition. Results from experimental runs were tested for significant differences with a two-sided Mann-Whitney U test ( $p < 0.05$ ).



Table 5.1 Number of individuals (n) of *Clupea harengus* (*C. har.*) and *Mnemiopsis leidyi* (*M. lei.*) per treatment in the mesocosm experiment, results with mean dry weight/wet weight ratio (DW/WW) of herring, standard deviation in parentheses, and significant ( $p < 0.05$ ) differences between treatments (marked with an asterisk). n.s. - not significant.

treatment	<i>C. har.</i> (n)	<i>M. lei.</i> (n)	DW/WW	<i>C. har.</i>	<i>C. har.</i> + <i>M. lei.</i>	<i>C. har.</i> + <i>M. lei.</i> double density
<i>C. har.</i>	6	0	0.203 ( $\pm 0.001$ )	-	n.s.	n.s.
<i>C. har.</i> double density	12	0	0.191 ( $\pm 0.001$ )	*	*	*
<i>C. har.</i> + <i>M. lei.</i>	6	32	0.201 ( $\pm 0.005$ )	n.s.	-	n.s.
<i>C. har.</i> + <i>M. lei.</i> double density	6	64	0.198 ( $\pm 0.004$ )	n.s.	n.s.	-

### 5.3. Results

Both *C. harengus* and *M. leidyi* were found in high abundances in the Sylt-Rømø Bight. While *C. harengus* reached its maximum abundance ( $2.3 \pm 1.4 \text{ ind.m}^{-3}$ ) in July, *M. leidyi* abundances increased steeply up to September (Fig. 5.2). In July and August both species were present at all sampling stations. In June, when *M. leidyi* abundance was still low, both species occurred only at one station simultaneously and in September, they both were found at 3 out of 5 stations (Fig. 5.2). The only sampling date when both species were found in higher abundances was in July. Here the proportion of *M. leidyi* to *C. harengus* was higher in the deeper parts (stations 2, 4 and 6) than in the shallower ones (stations 1, 3 and 5, Fig. 5.2).

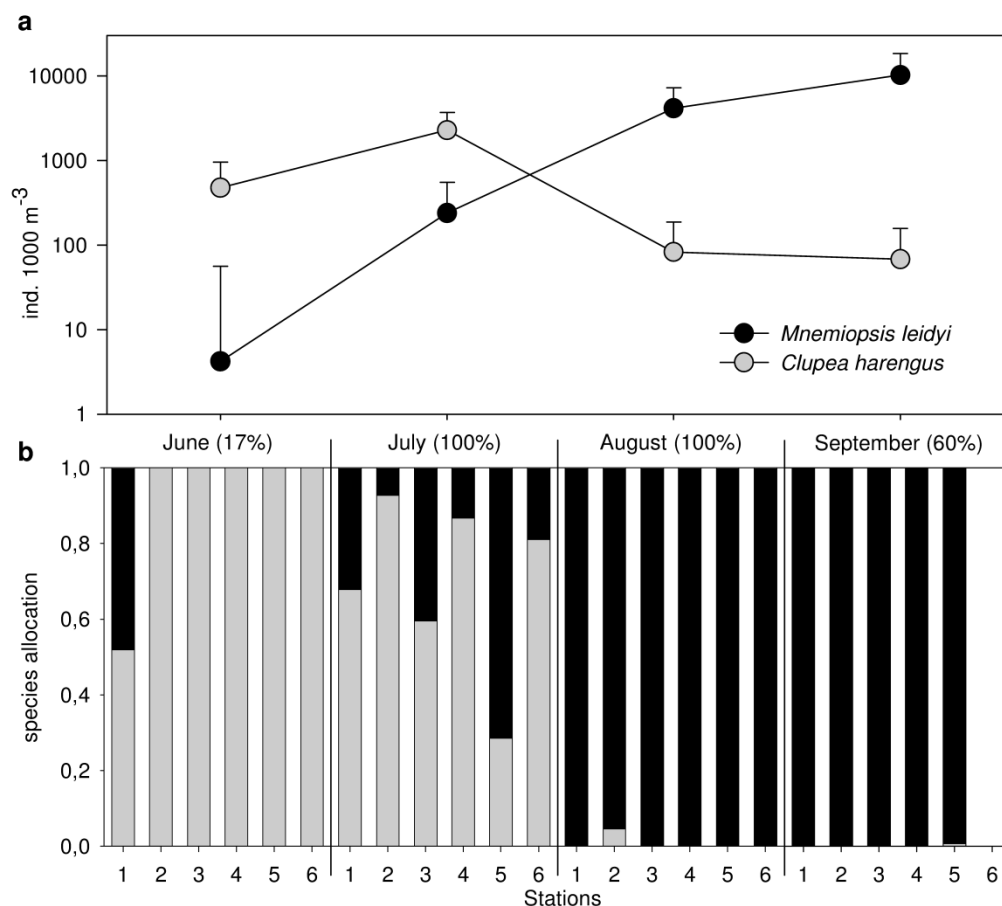


Fig. 5.2 Abundance of *Clupea harengus* and *Mnemiopsis leidyi* in the Sylt-Rømø Bight from June to September 2010 (a) in individuals 1000 m<sup>-3</sup> with standard deviation (only positive standard deviation is shown) calculated with weighted means considering the different depths of the bight by surface. (b) shows the proportion of *C. harengus* (grey bars) and *M. leidyi* (black bars) at the sampling stations during the study period. Percentage values in brackets indicate the percentage of stations where both *C. harengus* and *M. leidyi* occurred.

The size frequency distribution showed a higher proportion of large adult *M. leidyi* (>5 cm) in July than in the other months (Fig. 5.3). In August and September individuals <3 cm dominated in abundance. One cohort of *C. harengus* was present until September, when a second smaller cohort appeared (Fig. 5.3).

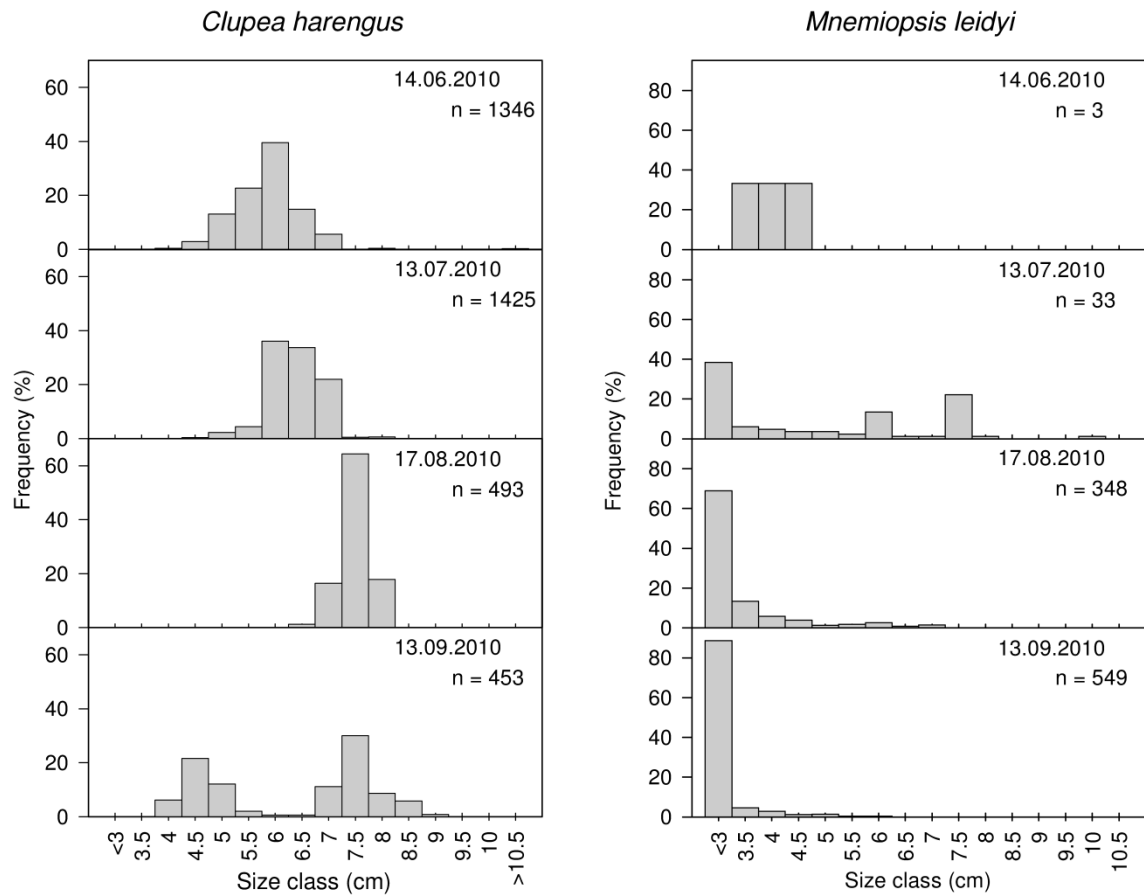


Fig. 5.3 Size structure of the *Clupea harengus* and *Mnemiopsis leidyi* population in the Sylt-Rømø Bight from June to September 2010.

The lowest over all zooplankton densities were found in June (Fig. 5.4) when nauplius stages of crustaceans were dominant in abundance. Highest zooplankton abundance was found in July (Fig. 5.4) and calanoid copepods dominated. In August and September the dinoflagellate *Noctiluca scintillans* was more abundant than calanoid copepods.

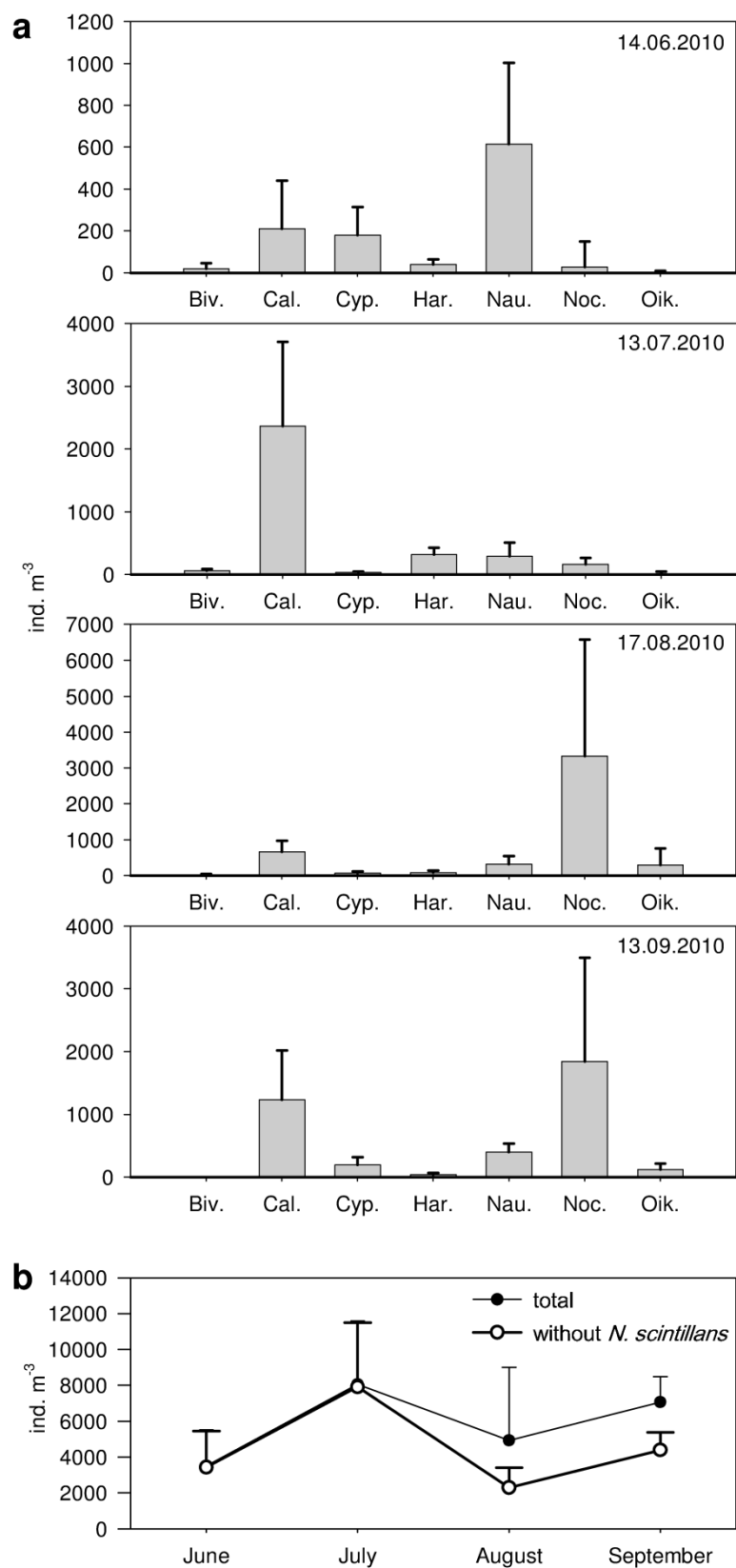


Fig. 5.4 Zooplankton abundance (a) of the seven dominant prey items of *Clupea harengus* and *Mnemiopsis leidyi* and (b) in total and without *Noctiluca scintillans*. For abbreviations of zooplankton organisms see Tab. 5.2.

Table 5.2 Diet of *Clupea harengus* (*C. har.*) and *Mnemiopsis leidyi* (*M. lei.*) in percent of volume in the Sylt-Rømø bight from June to September 2010. Total length (TL) with standard deviation (sd), size range (s. range) and number of analysed individuals (n) are given. Amp. - Amphipoda, Bel. – Bellerochea sp. (diatom), Biv. - Bivalvia larvae, CEx. - Cirripedia exuvia, Cla. - Cladocera, Cra. - *Crangon crangon*, Cyp. – Cypris larvae, Gas. - Gastropoda larvae, Har. - Harpacticoida, Hyd. - Hydrozoa, Meg. – Megalopa larvae, Mys. - Mysidacea, Nau. – Nauplii stages, Noc. - *Noctiluca scintillans*, Oik. - Oikopleura sp., Pol. - Polychaeta, Oth. - Other.

		TL	sd	s. range	n	Amp.	Bel.	Biv.	CEx.	Cla.	Cal.	Cra.	Cyp.	Gas.	Har.	Hyd.	Meg.	Mys.	Nau.	Noc.	Oik.	Pol.	Oth.
<b>Jun.</b>	<b>C. har.</b>	6.2	0.5	5.4-7.5	30	6.4	-	1.3	-	0.4	25.6	-	30.6	8.1	12.2	0.2	-	-	0.7	-	-	5.3	9.2
	<b>M. lei.</b>	4.4	-	4.1-4.7	2	-	-	-	-	-	28.3	-	3.8	2.9	8.4	-	-	-	21.3	35.0	-	-	0.3
<b>Jul.</b>	<b>C. har.</b>	6.4	0.4	5.5-7.3	25	0.9	-	0.5	-	0.3	66.6	-	3.0	0.6	18.3	-	3.1	-	1.2	-	-	3.8	1.8
	<b>M. lei.</b>	5.2	2.1	2.4-10	20	3.6	-	0.5	8.9	-	49.7	0.4	4.1	-	12.5	9.7	3.6	-	3.7	-	-	0.2	3.0
<b>Aug.</b>	<b>C. har.</b>	7.3	0.4	7-8.4	20	5.8	-	0.1	-	-	65.2	5.6	4.5	1.7	0.1	-	-	6.4	0.0	-	8.4	0.8	1.3
	<b>M. lei.</b>	4.2	1.7	1.6-8.3	27	-	-	47.2	3.0	6.8	11.1	-	10.7	0.8	-	-	-	3.4	4.9	-	4.2	4.8	3.1
<b>Sep.</b>	<b>C. har.</b>	7.6	1.0	5.8-9.5	14	8.1	1.7	0.1	-	-	51.8	-	10.9	-	7.2	-	-	-	10.0	-	-	-	9.9
	<b>M. lei.</b>	3.8	1.0	1.6-5.9	28	-	6.6	15.5	-	-	35.3	-	4.7	1.7	8.0	-	-	2.5	16.4	1.2	1.7	-	6.4

Table 5.3 Interspecific ( $O_{jk}$ ) and mean intraspecific diet overlap values of *Clupea harengus* ( $O_j$  *C. har.*) and *Mnemiopsis leidyi* ( $O_k$  *M. lei.*) with range found by the method of Wallace and Ramsey (1983).

	$O_{jk}$	$O_j$ <i>C. har.</i>	$O_k$ <i>M. lei.</i>
June	-	0.88 (0.77 - 0.97)	-
July	0.96	0.99 (0.94 - 1)	0.86 (0.69 - 0.97)
August	0.25	0.96 (0.92 - 0.99)	0.91 (0.84 - 0.97)
September	0.88	0.89 (0.75 - 0.97)	0.93 (0.89 - 0.97)

Diet overlap was not calculated for samples in June, when the abundance of *M. leidyi* was low and hence the sample size was small. While calanoid copepods ranked second with 25.6 % and 28.3 % of the food for *C. harengus* and *M. leidyi* respectively, they differed in their main diet (Tab. 5.2). Cypris larvae represented 30.6 % of the volume of the gut contents of *C. harengus* and *N. scintillans* represented 35 % of the gut contents of *M. leidyi*. The highest diet overlap between herring and jellyfish was measured in July (Tab. 5.3). At this stage calanoid copepods were the main food resource for both *M. leidyi* and *C. harengus* (Tab. 5.2) with harpacticoid copepods ranking second in both species. Bivalve larvae (47.2 %) accounted for a high proportion of the food of *M. leidyi* in August. *C. harengus* fed on a similar proportion on calanoid copepods as in July. The lowest overlap values were found in August (Tab. 5.3). For both species calanoid copepods were again the main food source in September, followed by cypris and nauplii larvae for *C. harengus* and *M. leidyi* respectively.

For *C. harengus* significant positive selection for copepods and cypris larvae could be found, except for Harpacticoida in August, Calanoida in September as well as in June and August at 2 stations, where cypris larvae were negatively selected (Fig. 5.5). For *N. scintillans*, nauplii larvae and Oikopleura selection was negative or neutral at most stations.

For *M. leidyi* no significant or negative selection for *N. scintillans* was found. Selection for other zooplankton organisms differed between months. In July *M. leidyi* selected against Bivalvia larvae at one station and no significant selection was found at the others, but in August and September significant selection for Bivalvia larvae was found at all stations (Fig. 5.5).

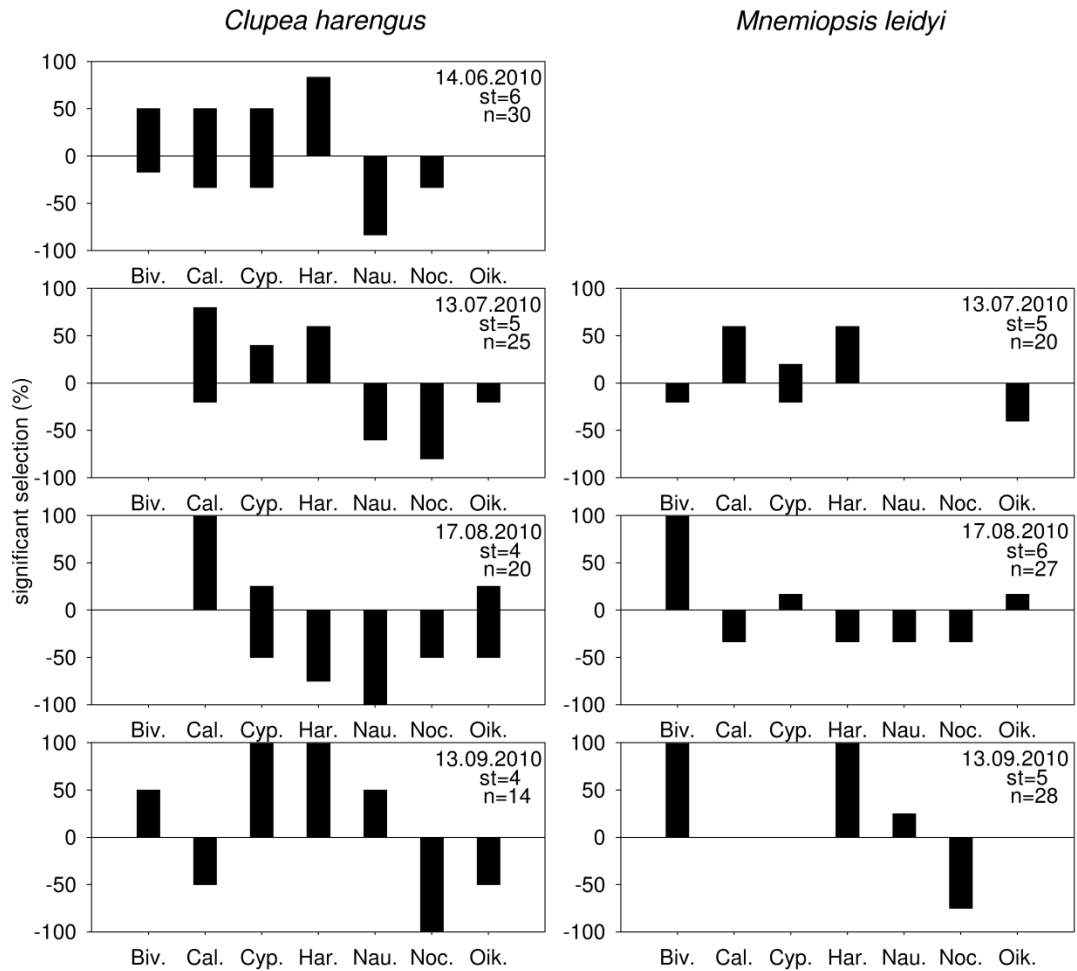


Fig. 5.5 Selection of zooplankton prey by *Clupea harengus* and *Mnemiopsis leidyi* in the Sylt-Rømø Bight in percentage of stations with significant selection. Positive values signify positive selection and negative values signify avoidance. st – number of stations, n – number of analysed individuals. For abbreviations of zooplankton organisms see Tab. 5.2.

Results from stable isotope analysis showed significant higher  $\delta^{15}\text{N}$  values for *C. harengus* than for *M. leidyi* (Fig. 5.6). *Mnemiopsis leidyi* was significantly more depleted in  $^{13}\text{C}$  as *C. harengus*. No significant differences were found between  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values of *C. fornicata* and *E. americanus* (Fig. 5.6). The calculations of trophic levels based on the stable isotope analysis resulted in a trophic level of 3.08 for *C. harengus* and 2.47 for *M. leidyi*.

Condition of herring at the end of the experiments was indicated by the DW/WW ratio of body mass. This ratio was lowest in the treatment with 12 *C. harengus* and increased in the treatments with 64 *M. leidyi*, 6 *C. harengus* and 32 *M. leidyi*, 6 *C. harengus*. The

highest DW/WW ratio was found in the treatment with 6 *C. harengus*. Differences between the DW/WW ratios were tested by Mann-Whitney-U test and showed only significance ( $p < 0.05$ ) between the treatment with 12 *C. harengus* and all the other treatments (Tab. 5.1).

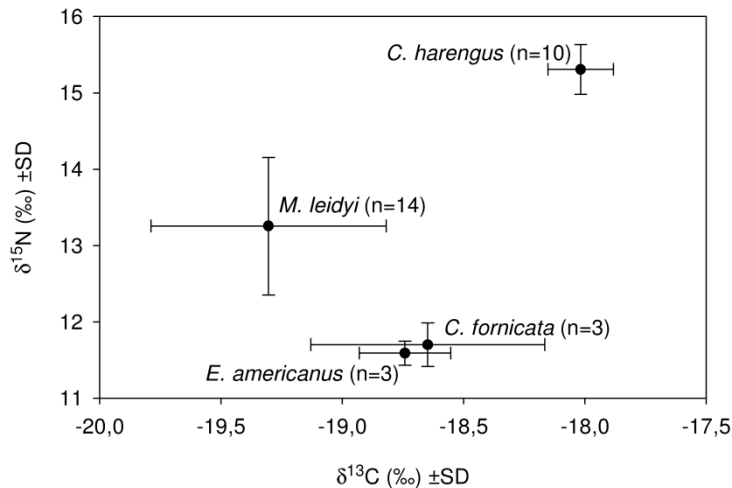


Fig. 5.6 Stable isotope signature of *Clupea harengus*, *Mnemiopsis leidy*, *Crepidula fornicata* and *Ensis americanus* in the Sylt-Rømø Bight.

#### 5.4. Discussion

The most reliable comparisons of dietary overlap are those obtained by sampling specimens both at the same location and time. The main results of this study suggest low potential of competition in the Wadden Sea area due to the low temporal overlap of the occurrence of *M. leidy* and *C. harengus*. Also other planktivorous fish had their maximum abundance in spring (Kellnreitner et al. 2011), when *M. leidy* abundance was still low. Exceptions are *Atherina presbyter* and *Engraulis encrasicolus*, which are Lusitanian species and inhabited the bight only in summer and autumn. A comparison of our results with those from the 1990s (Herrmann et al. 1998) revealed a change of abundance peaks of *C. harengus* from autumn to spring (Kellnreitner et al. 2011). This change was unlikely caused by *M. leidy*, as multiple other factors may interfere. Nevertheless, this change may be beneficial for *M. leidy* population development. Data from a long-term *M. leidy* survey showed a doubling of the population in October and a sharp decline during November (Sylt Bight Ecological Time Series). *Clupea harengus*



abundance in October and November was lower than in September (Kellnreitner and Pockberger unpub. res.).

The dominance of small size classes of *M. leidy* in the Wadden Sea is in accordance with observations in other invaded areas (Javidpour et al. 2009b; Riisgård et al. 2007). In native habitats, larger *M. leidy* were found in a higher proportion (Burell and Van Engel 1976; McNamara et al. 2010). The dominance of smaller size classes could be related to a short but strong reproduction period, to a lack of suitable food for larger size classes or to insufficient amounts of food. Causes could be either intraspecific competition or competition with other organisms for food or else a low availability of zooplankton in general. Small stages of *M. leidy* have comparatively higher clearance rates per unit weight than larger stages (Kremer 1979). Dominance of small individuals of *M. leidy* means high predation pressure on zooplankton. The population in Limfjorden, which consumed high amounts of copepods, was composed mainly of small individuals at very high densities (up to 867 ind. m<sup>-3</sup>) (Riisgård et al. 2007). In the Sylt-Rømø Bight, besides *M. leidy*, high abundances of *Rhizostoma pulmo* are frequently observed in August (Kellnreitner and Pockberger pers. obs.), which can be responsible for the drop of zooplankton abundance in this month. Data obtained by long term series starting in the 1980s indicate a drop of zooplankton abundances in the 2000s (P. Martens, Sylt Bight Ecological Time Series). Especially abundances of adult copepods seem to have diminished in recent years. Further research is needed to investigate whether this is caused by increased predation by jellyfish or if other factors are involved.

In recent years population development of *M. leidy* in the Wadden Sea seemed to be similar to the situation in the Sea of Azov, where *M. leidy* was unable to survive cold winters. Every year re-colonisation by spring water import from the Black Sea took place (Volovik et al. 1993). The most important conditions for the development of *M. leidy* are temperature and food availability (Kremer 1994; Oguz et al. 2008). Costello et al. (2006) and Sullivan et al. (2001) found a significant correlation between spring temperatures and *M. leidy* abundance in Narragansett Bay, USA. In the northern Wadden Sea the winter 2009/10 was exceptionally cold, with temperatures below 0°C and drift ice temporally covering the bight. In 2010 the first individuals of *M. leidy* appeared in June, whereas in 2008, after a mild winter, first individuals were observed already in January (Fischer, 2008). Densities measured up to the beginning of August in 2008 were twofold higher than the maximum densities registered in August 2010.

Whenever both species were present, the diet overlap between *M. leidy* and *C. harengus* was temporarily very high, which was related to feeding on large proportions of

copepods in July and September. In fact, copepods are important food resources for *M. leidyi* both in native and in invaded habitats (Burell and Van Engel 1976, Mutlu 1999; Zaika and Revkov 1998). Likewise, the importance of copepods for planktivorous fish in the Wadden Sea is well known (Elliott and Dewailly 1995; Hicel 1975; Last 1987; Rauck and Zijlstra 1978). Kellnreitner et al. (2011) found a calanoid copepod eating guild consisting of 7 fish species in summer and autumn. The most abundant species were *Ammodytes tobianus* and *C. harengus*.

The low diet overlap in August was related to the high ingestion of bivalve larvae by *M. leidyi*. In the Sylt Rømø Bight in August bivalve larvae are dominated by the Pacific oyster *Crassostrea gigas*, an introduced species in the Wadden Sea. Oyster larvae of *Crassostrea virginica* seem to be a dominant prey in the native range of *M. leidyi* (Kremer 1979). At all sampling sites in August a positive selection of *M. leidyi* on bivalve larvae was found whereas a positive selection of *C. harengus* on copepods was observed. Feeding mechanisms of *C. harengus* are related to the density of zooplankton (Gibson and Ezzi 1985). *C. harengus* switches from filter-feeding at high prey densities to particle-feeding at lower densities. Batty et al. (1990) and Sandström (1980) showed selective feeding of *C. harengus* on larger zooplankton prey. The selectivity of *M. leidyi* is mainly related to the feeding mechanism. Prey density, motility and the escaping potential of the prey are important (Madsen and Riisgård 2010). As a result, significantly lower selection was found in *M. leidyi* as in *C. harengus*. In September diet overlap increased again with higher copepod abundance. No diet overlap was calculated for June due to the low sample number of *M. leidyi* and hence to the poor characterization of the diet.

The results from the stable isotope analysis point to large amounts of phytoplankton food in *M. leidyi*. We found large diatoms (chains with a diameter of 70 µm and length up to 1.5 mm) in the diet of *M. leidyi* but we did not find smaller phytoplankton. The higher depletion in <sup>13</sup>C in *M. leidyi* could be an indication for a closer link to the plankton food chain as planktivorous fish were also more depleted in <sup>13</sup>C as benthic fish (Kellnreitner, unpub. res.).

The results of the experiments imply that intraspecific competition in *C. harengus* is more important than competition with *M. leidyi* at the presented zooplankton densities. In our experiment zooplankton densities close to *in situ* densities were chosen. These densities were most likely to high to cause a significant decrease in body condition of herring related to competition with *M. leidyi*. Competition takes place if a common resource is scarce. We could show that *C. harengus* and *M. leidyi* use the same resources most of

the time. Bilio and Niermann (2004) and Gucu (2002) come to the conclusion that it is low competition with planktivorous fish due to overfishing which is partly responsible for the mass occurrences of *M. leidy* in the Black Sea. Additional experiments are needed to show the impact of competition with planktivorous fish on the nutritional condition of *M. leidy* and the effect of stronger food limitation on competition between the two species. An important step towards the understanding of the feeding relationship will be the assessment of the amount of zooplankton consumed by *C. harengus* and by *M. leidy* in this area.

The importance of the Wadden Sea as nursery area for *C. harengus* and many other North Sea fish requires an early assessment of the possible threats induced by *M. leidy*. The consumption of high amounts of copepod production observed in other areas and the high diet overlap with *C. harengus* makes *M. leidy* a potential competitor. To date we could not find predators preying on *M. leidy* in higher amounts. The amount of a mass occurrence depends on the environmental conditions, food availability and the competition for food. Due to their temporarily high diet overlap *C. harengus* and other planktivorous fish might just as well be important competitors for *M. leidy*. This has to be taken into consideration in fisheries management decisions, since healthy planktivorous fish stocks might be an important factor in the control of *M. leidy* mass occurrences.

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## **6. Resource partitioning between juvenile herring (*Clupea harengus*) and sand-smelt (*Atherina presbyter*) in the Wadden Sea, North Sea?**

Florian Kellnreitner, Moritz Pockberger, Harald Asmus, Patrick Polte

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### **Abstract**

Multi-national assessments of fish community status in the Wadden Sea accomplished during the mid 1990's, described the sand smelt (*Atherina presbyter*) as a relatively rare visitor in these shallow tidal waters at the Eastern North Sea coast. Since 2001 when regular fish sampling on Wadden Sea tidal flats was established at the German Island of Sylt, multiple ontogenetic stages of the species, including larvae, juveniles and adult fish could be detected in high abundance. In this study, we address the questions whether a thriving component in the pelagic zone of a shallow water system might compete for food with the commercially important herring (*Clupea harengus*). Results of *in situ* analyses on plankton availability, gut contents and stable isotope composition are combined with mesocosm experiments to gain insight of the potential interactions between the two dominant planktivorous fish species.

Our results of diet analyses and experimentation in mesocosms indicate that young of the year herring feeds primarily on calanoid copepods, whereas sand smelt of similar size preferred barnacle larvae when available. The diet of both species however shifted towards copepods or barnacle larvae respectively, when the one or the other prey became limited. Given a suitable food supply, results indicate a resource partitioning among herring and sand smelt rather than significant prey overlap. Both species might generally profit from high meroplankton densities induced by benthos recruitment in Wadden Sea waters.

### **Keywords**

Zooplankton, sand smelt, herring, mesocosm, Wadden Sea, North Sea

## 6.1. Introduction

The extended tidal flats and shallow water zones of the Wadden Sea are generally considered as important nursery and foraging areas for North Sea fish (Rauck and Zijlstra 1978). Atlantic herring (*Clupea harengus*) is the dominant pelagic fish using Wadden Sea waters as a nursery and is considered primarily recruiting from North Sea autumn and winter spawning populations (Corten 1986, Daan et al. 1990), although local stocks of spring spawners occur in the Wadden Sea (Polte and Asmus 2006a). Large aggregations of young of the year individuals can be frequently observed in shallow bays and harbor basins during early summer (pers.obs.) where they feast on copepods and other zooplankton prey (Herrmann et al. 1998, Kellnreitner et al. 2011). Although subject of common knowledge, scientific studies of the Wadden Sea's role in the life cycle of pelagic species such as herring are rather scarce although the species represents a key component within temperate, coastal food webs as well as in commercial fisheries in Europe (Greenstreet et al. 1997, Simmonds 2007,). However, an immense inter-annual variation of herring recruitment demonstrated for stocks worldwide (Zheng 1996) is likewise documented for the generally high recruitment in the Wadden Sea area (Philippart et al. 1996). Although environmental variables structuring recruitment variability are not yet satisfyingly understood, there is some consensus on bottlenecks in early life stages - such as suitable zooplankton prey availability at the point of first feeding (Cushing 1975, Pederson et al. 1990, Fossum 1996) and in the first year of life (Norcross et al. 2001) - where recruitment strength is determined (Axenrot and Hansson 2003, Nash and Dickey-Collas 2005). Limitation of food resources may be related to abiotic environmental effects as well as on predator interactions. Corten (1986) assumed that low recruitment of North Sea herring during the late 1970s was caused by unusual hydrological conditions which caused a disruption of the transport of herring larvae to their nursery grounds. He supposed that most of the larvae were thus bound to areas with unfavorable conditions, such as low food supply. In Prince William Sound (Alaska) Norcross et al. (2001) related high mortalities of 0+ pacific herring (*Clupea pallasii*) to low zooplankton availability during winter months. Food limitation can also result from competition of multiple predators for a common resource. Lynam et al. (2005) concluded that competition by jelly fish might have a negative impact on herring recruitment in the North Sea. In the Baltic Sea Casini et al. (2006) found a correlation between high abundance of Clupeids (herring and sprat, *Sprattus sprattus*) and low zooplankton abundance and also low body condition of both species. As both species feed on the same zooplankton prey Casini et al. (2006) infer that competition is the density dependent factor impacting body condition of the Clupeids.

Recently, during the past decade high densities of sand smelt (*Atherina presbyter*) were observed in the northern Wadden Sea. Observations include all life stages of the species which accounts for successful reproduction in the area (Polte 2004). Since *A. presbyter* is commercially irrelevant in the North Sea region, the historical status of this species in Wadden Sea waters is poorly documented. Reconstruction of the demographic history of *A. presbyter* based on mitochondrial DNA analysis indicates an evolutionary very recent population of the Wadden Sea area that might have possibly occurred more recent than the 17<sup>th</sup> century (Francisco et al. 2009). However, during the most recent assessment of the status of Wadden Sea fishes, published in 1996 as a trilateral effort of the Netherlands, Germany and Denmark, *A. presbyter* stocks were classified as susceptible in the Dutch Wadden Sea, absent in the German part and it was unknown if the species occurred at all on the Danish Wadden Sea coasts (Berg et al. 1996). Then, in the period from 2001 to 2006, own observations include *A. presbyter* as a dominant pelagic species in coastal waters of the Island of Sylt in the German part of the northern Wadden Sea (Polte and Asmus 2006b). Although it might not be possible here to determine the exact age and origin of the *A. presbyter* population inhabiting the Wadden Sea, it seems obvious that the abundance of the species has significantly increased in the area and that today the species is established as a component of the Wadden Sea fish assemblage. The reasons for the expansion of the species in the Wadden Sea area remain subject of speculation but they might be linked to climate change related sea surface warming (Walther et al. 2002, Rose 2005, Engelhard et al. 2011).

The sand smelt is a fast growing, short living fish species with coastal distribution. Sand smelt live up to a maximum of four years. About 60% of the maximum size of 15 cm is reached in the first year of life and in the following years most of the energy is used for reproduction (Lorenzo and Pajuelo 1999). Quantitative dietary data on the sand smelt is scarce, especially in its northern distribution range. The sand smelt is known as an opportunist feeding on a broad range of benthic and pelagic prey (Kislalioglu and Gibson 1977, Turnpenny et al. 1981, Moreno and Castro 1995, Pombo et al. 2002, Pombo et al. 2005). Especially in marine environments the diet of sand smelt includes pelagic copepods and larvae of invertebrates (Kislalioglu and Gibson 1977, Turnpenny et al. 1981, Moreno and Castro 1995) which are also food resources for the herring (Last 1987, 1989). Although both species feed on zooplankton to a certain extent they can differ in their feeding mode as the herring has the possibility to switch between filter- and particulate-feeding (Gibson and Ezzi 1985) while sand smelt is assumed to be restricted on particulate-feeding (Turnpenny et al. 1981). In a study on Wadden Sea fish feeding guilds Kellnreitner et al. (2011) found a high share of zooplankton in the diet of sand

smelt and during summer months sand smelt was present in the same feeding guild as juvenile herring.

We therefore assume that with increasing abundance of sand smelt new feeding interactions with zooplanktivorous fish of the northern Wadden Sea may arise. Using a combination of field surveys and experimental mesocosm studies the following hypotheses are tested: i) The trophic spectrum of herring and sand smelt does overlap resulting in a potential competition for zooplanktonic prey, ii) Differences in diet composition are based on species specific selection of zooplankton prey items, and iii) The fast growing sand smelt is a significantly more efficient zooplankton predator in respect of individual predation per time unit.

## 6.2. Materials and methods

### 6.2.1 Study sites

Studies were conducted on the east coast of the Island of Sylt in the northern Wadden Sea (North Sea). The Sylt-Rømø Bight (54°50'–55°10' N, 8°20'–8°40'E) is a shallow tidal basin formed by the islands of Sylt (Germany) and Rømø (Denmark). Along the tidal watersheds the Sylt-Rømø Bight is nearly closed by solid causeways connecting the islands with the mainland. A single, 2 km wide inlet connects the bight to the open North Sea. Tidal flats represent one-third of the bight's 407 km<sup>2</sup> area. Tides are semi-diurnal with a mean range of about 2 m. Salinity is subjected to seasonal variations between 28 (winter) and 32 (summer). Mean water temperatures vary seasonally between 0 °C and 20 °C (Gätje and Reise 1998). Samples were taken during August and September in 2006, 2008 and 2010. The average water surface temperature was 19 °C.

### 6.2.2 Zooplankton sampling

In 2006 we took zooplankton samples using a 2.5 m long bongo net (double net ring with two identical nets horizontally mounted) with an opening diameter of 0.6 m and a mesh size of 250 µm. The net was towed horizontally for 5 minutes in surface waters at a depth of 1 m with a speed of 2 knots. The water volume sampled was measured by a flow meter attached to one of the nets openings. Using the bongo net, each haul results in two samples of identical water volume. Samples were subsequently sieved over mesh sizes of 500 µm and 250 µm. The sample fraction remaining in the 250 µm mesh

represented the target plankton size between 500 and 250  $\mu\text{m}$ . The zooplankton sampled was subjected to different treatments: (i) Organisms were carefully washed into buckets with filtered sea water for transport to mesocosm basins that were equipped with a defined amount of the sampled zooplankton immediately after sampling. (ii) Samples were washed into bottles and subsequently fixed by freezing at  $-20\text{ }^{\circ}\text{C}$  ( $n= 6$ ). In 2008 and 2010 zooplankton samples were taken in the framework of an extended time series where zooplankton samples are taken twice a week. 35 L of surface water were filtered, washed into a bottle and fixed with 5% formalin for later identification. The average of three consecutive samples was used for calculations.

### 6.2.3 Fish sampling

In 2006 fish for mesocosm experiments and gut content analysis were sampled 2m below the mean low tide level in the shallow subtidal zone using a beach seine (9 m long, 2 m high, mesh size: 6 mm). The length of each haul was 40 m resulting in an area of approximately 360  $\text{m}^2$ . In 2008 and 2010 fish were obtained in the shallow subtidal zone (2-5 m depth) using the beach seine as well as a trawl (7 m long, 3 m high, mesh size in the cod end: 6 mm) operated from a research vessel. Fish were identified, total length measured to the nearest mm and wet weight to the nearest 0.1 g.

### 6.2.4 Mesocosm experiments

*Mesocosm set up:* Eight round 2  $\text{m}^3$  tanks were set up indoors a greenhouse with natural light conditions. The mesocosms were connected to an open seawater circuit fed by a water pump stationed submerged at 2 m below mean low tide level at the North-East coast of the Island of Sylt. In- and outflows of the mesocosm tanks were filtered by 250  $\mu\text{m}$  mesh to prevent contamination with zooplankton of the studied size class transported by inflowing seawater and, respectively the loss of experimentally induced zooplankton densities by the tanks outflow. Using the open circuit system temperature and salinity could be kept at *in situ* levels throughout the experimental period. To maintain constant water levels and prevent overflow caused by blocked filters, aquarium air pumps were installed at each tanks outflow supplying constant turbulence to the filtering mesh. Inflows to the tanks were situated about 40 cm above the water level to provide sufficient aeration and to create a slowly circulating water body.

*Experimental design:* Each tank was provided with the particular amount of zooplankton corresponding to the volume sampled by one haul with the bongo net. After a 2 day adaptation period a random 10 L plankton sample was taken out of each tank to define a

reference abundance without any predators present. Immediately after taking the reference samples, 5 (0-group) individuals of one fish species were added to each of 4 tanks while the remaining 4 tanks were used as predator-free controls. Consecutive plankton samples were taken from all tanks 48 and 72 hours after exposure to fish predation. Fish were then removed from the tanks and frozen at -20 °C for later analyses of gut contents. For both fish species the experiment was conducted two times consecutively and data were pooled for statistical analysis (2 x 4 predator tanks; 2 x 4 control tanks). Results were tested for significant differences in zooplankton abundance between tanks with fish and reference tanks with an unpaired t-test ( $p < 0.05$ ). To avoid artifacts due to differing initial zooplankton densities, abundance data were transformed by dividing abundance of each tank by the average of all reference tanks of an experiment at the given time. Results are therefore presented as ratio between reference tanks and tanks with fish.

#### 6.2.5 Gut content analysis

Analysis of gut contents was conducted on all fish used for mesocosm experiments and on an identical number of fish directly stored after beach seine fishing in the field in 2006 as well as on the fish taken in the following years of 2008 and 2010. The entire contents were removed from the digestive system, diluted in 10 ml seawater, and homogenized. The solution was transferred into a Bogorov counting chamber and zooplankton organisms were identified to the highest possible taxonomic separation and quantified under a stereo microscope. Due to the high degree of body fragmentation of digested prey organisms, counting was limited to slow-digestible individual *caput* sections.

#### 6.2.6 Diet overlap and prey selectivity

The proportion (%) of the items of each prey category relative to the total number in the gut was calculated for each analyzed individual. Diets are expressed as the mean of this proportion per fish species and sample. Diet overlaps were calculated using Pianka's niche overlap index (Pianka 1973)

$$O_{jk} = O_{kj} = \frac{\sum_i^n p_{ij} p_{ik}}{\sqrt{\sum_i^n p_{ij}^2 \sum_i^n p_{ik}^2}}$$

where  $p_{ij}$  and  $p_{ik}$  are the proportions of the  $i^{\text{th}}$  prey type used by the  $j^{\text{th}}$  and the  $k^{\text{th}}$  species respectively. The output values result between 0 (no overlap) and 1 (complete overlap).



A good characterisation of diets is required to draw conclusions from diet overlaps between two species. We used the method proposed by Wallace and Ramsey (1983) where samples of each species within a month are randomly divided 30 times in two sets and each time the diet overlap is calculated to assess intraspecific diet overlap. A high intraspecific diet overlap means low variation within samples and therefore good characterisation of diets (Wallace and Ramsey 1983).

Prey selectivity for both fish species was assessed using Pearre's selectivity index (Pearre 1982)

$$C = \left( \frac{\chi^2}{n} \right)^{\frac{1}{2}}$$

based on the  $\chi^2$  notation

$$\chi^2 = \frac{n(|a_d b_e - b_d a_e| - n/2)^2}{abde}$$

where  $a$  is the number of individuals of prey species  $a$  and  $b$  is the sum of all the other prey species except species  $a$  in the diet (subscript  $d$ ) and the environment (subscript  $e$ ) respectively.  $a = a_d + a_e$ ,  $b = b_d + b_e$ ,  $d = a_d + b_d$ ,  $e = a_e + b_e$  and  $n = a_d + a_e + b_d + b_e$ .

### 6.2.7 Stable isotope analysis

In September 2010 a sample of 12 herring and 12 sand smelt was used for analysis of stable isotope composition of carbon and nitrogen. Dorsal white muscle tissue was removed from the fish directly after catch and measurement of biometrics. Samples were freeze dried, ground to a fine powder using a ball mill, encapsulated in tin capsules, weighted and sent to the Museum for Natural History in Berlin, Germany for further processing. Samples were processed in a THERMO/Finnigan MAT V isotope ratio mass spectrometer, coupled to a THERMO Flash EA 1112 elemental analyzer via a THERMO/Finnigan Conflo III- interface with a precision better than 0.15‰. Results are represented in the delta notation using Vienna Pee Dee Belemnite (VPDB) for carbon and atmospheric air (AIR) for nitrogen as standards. Resulting  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values were tested for significant differences between herring and sand smelt using an unpaired two sample t-test ( $p < 0.05$ ).

### 6.3. Results

During August 2006 calanoid copepods ( $3.51 \pm 1.15$  individuals  $L^{-1}$ ) were the most abundant taxon in zooplankton samples (Fig. 6.1). They represented 86.3% of all organisms identified in samples. During September 2006 larval stages of barnacles were found in higher abundances than in August. In fact, they made up to 49.3% of zooplankton in the samples with nauplius larvae as the dominant stage ( $2.83 \pm 2.05$  individuals  $L^{-1}$ ). Calanoid copepod abundance dropped to less than a third ( $1.02 \pm 0.64$  individuals  $L^{-1}$ ) of its August abundance. In September 2008, a high abundance of calanoid copepods ( $11.2 \pm 11.47$  individuals  $L^{-1}$ ) was observed and harpacticoid copepods were more abundant than in other years (Fig. 6.1). Also in September 2010 calanoid copepods were the most abundant zooplankton taxon where they represented 77.5% of all identified zooplankton organisms.

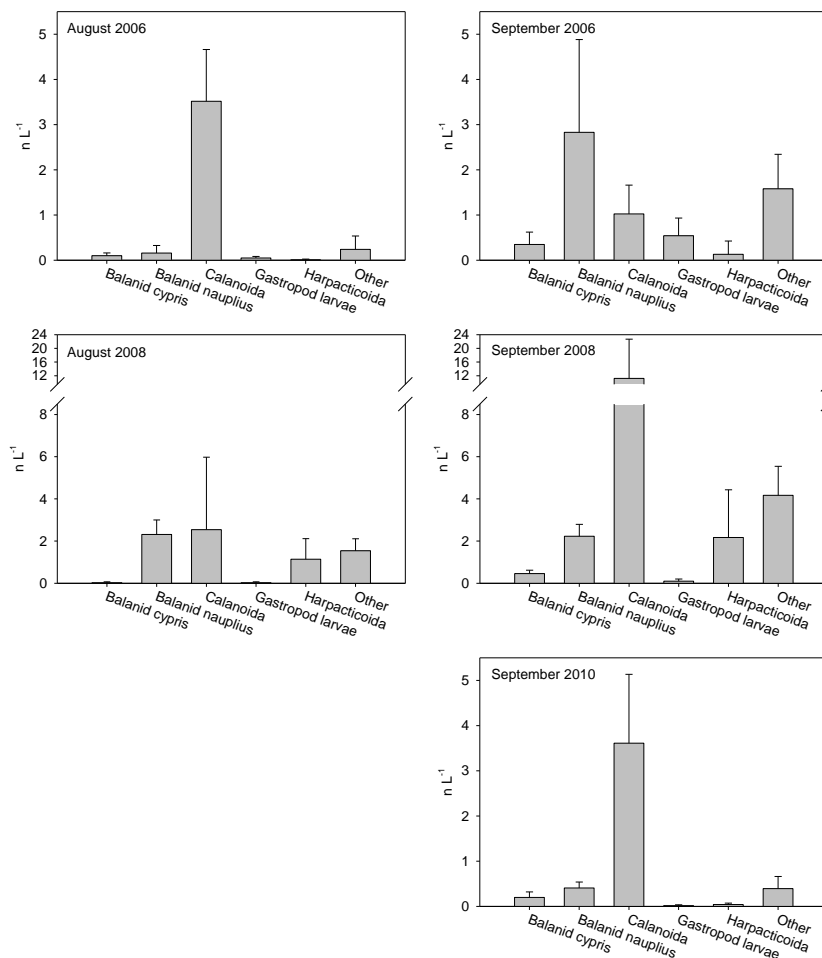


Fig. 6.1 Abundance of zooplankton organisms in individuals per liter ( $n L^{-1}$ ) sampled in the Sylt-Rømø Bight. The most important prey items of *Clupea harengus* and *Atherina presbyter* are shown, the others are pooled (Other).

Tab. 6.1 Size range and mean total length [cm] of *Clupea harengus* and *Atherina presbyter* found in the samples of different years.

	range (cm)	mean±sd (cm)
<b><i>C. harengus</i></b>		
August 2006	(6-8)	7.36±0.59
September 2006	(7-8)	7.56±0.42
August 2008	(5.5-8.5)	6.88±0.52
September 2008	(6-9)	8.41±0.51
September 2010	(5.8-9.5)	7.51±0.86
<b><i>A. presbyter</i></b>		
August 2006	(5-7)	6.40±0.56
September 2006	(6.5-9)	7.40±0.60
August 2008	(3.5-8)	6.54±0.90
September 2008	(5.5-9.5)	7.47±0.75
September 2010	(4.5-8.9)	6.93±0.98

Average total lengths of herring and sand smelt present in the catches and used for the experiments were  $7.54 \pm$  cm and  $6.95 \pm$  cm, respectively (Tab. 6.1).

Diets of herring and sand smelt are presented in figure 6.2. Herring fed mainly on calanoid copepods, except for September 2006 where barnacle cypris larvae were the most frequent prey (74.4%). Inversely, barnacle larvae (cypris and nauplius) were the most common prey found in the diet of sand smelt. Only in August 2008 both species fed on high amounts of calanoid copepods (Fig. 6.2). Harpacticoid copepods, gastropod veligers and other zooplankton were only found in minor quantities in the diets of both species.

Herring showed either positive selection or no significant selection for calanoid copepods (Tab. 6.2). They were the only analyzed prey group never avoided by herring during our investigation. Nauplius larvae of barnacles and gastropod larvae were avoided or not selected by herring. Sand smelt showed positive selection for barnacle cypris larvae, except for August 2006 when they were not significantly selected. Calanoid copepods were avoided most of the time, but positively selected during August 2008. Gastropod larvae were either not selected or avoided by the sand smelt (Tab. 6.2).

Both species showed high (>0.8) intraspecific diet overlap in all years and months sampled. This signifies good characterization of diets and therefore high significance of interspecific diet overlaps. High diet overlaps between species were found in September

2006 and August 2008 (Tab. 6.3). During the other sampling periods overlap was low, with the lowest overlap in September 2008.

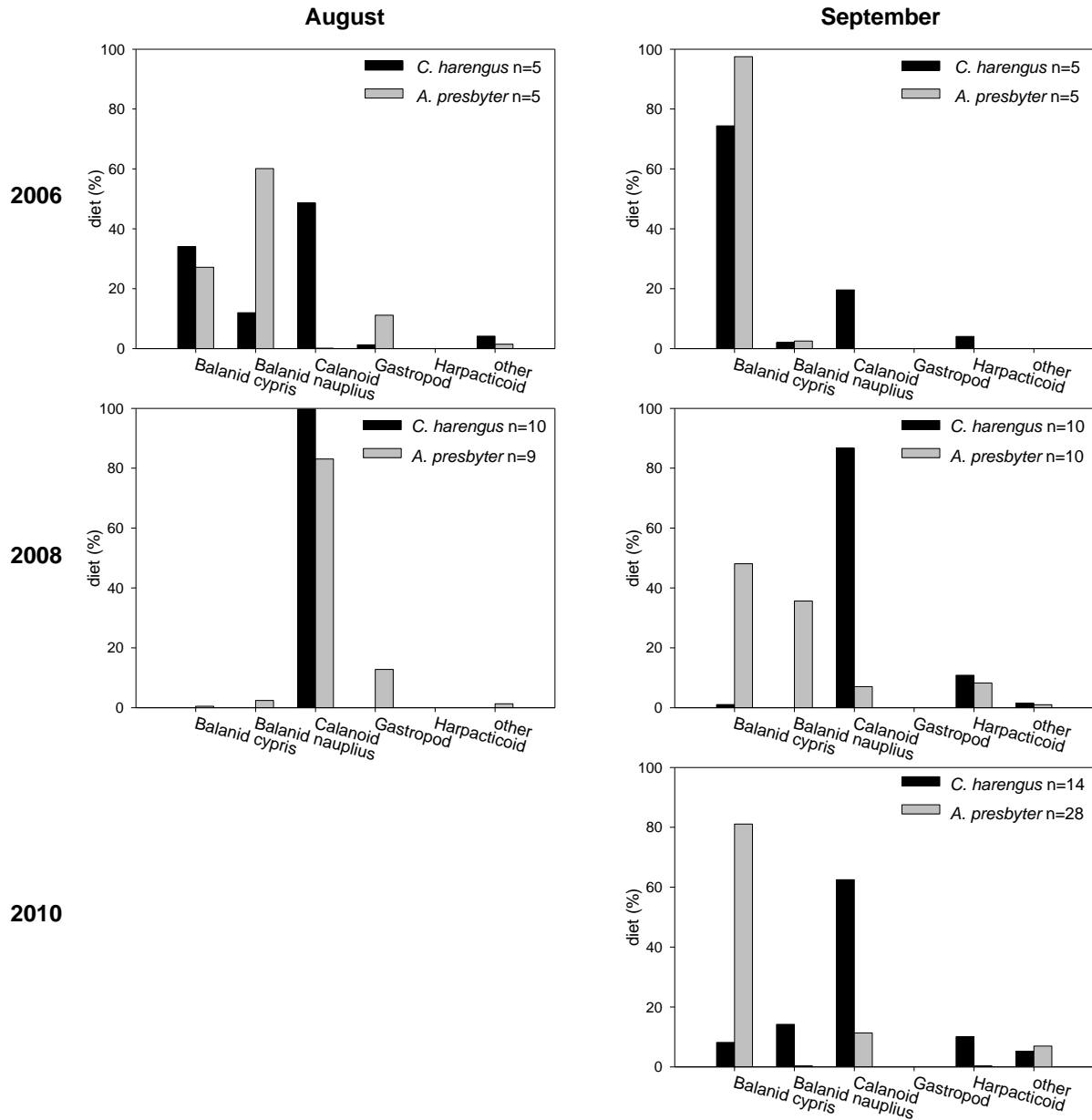


Fig. 6.2 Diet composition in percentage of prey items found in the guts of *Clupea harengus* and *Atherina presbyter* caught in beach seine and trawl samples. The five most abundant taxa are shown and the rest is grouped as „other“.

Tab. 6.2 Diet selection of *Clupea harengus* and *Atherina presbyter* calculated by Pearre's (1982) selectivity index. Significant ( $p < 0.05$ ) positive selection (+) and significant ( $p < 0.05$ ) avoidance (-) are shown for the five most abundant prey taxa. n.s. – not significant. Bal. – Balanid.

	2006		2008		2010
	Aug.	Sep.	Aug.	Sep.	Sep.
<b><i>Clupea harengus</i></b>					
Bal. cypris larvae	n.s	+	-	n.s	n.s
Bal. nauplius larvae	n.s	-	-	-	n.s
Calanoida	n.s	n.s.	+	+	n.s
Gastropod larvae	-	n.s	-	-	-
Harpacticoida	+	n.s	-	n.s	n.s
<b><i>Atherina presbyter</i></b>					
Bal. cypris larvae	n.s	+	+	+	+
Bal. nauplius larvae	+	-	-	+	n.s
Calanoida	-	-	+	-	-
Gastropod larvae	n.s	n.s	n.s	-	-
Harpacticoida	+	-	-	n.s	-

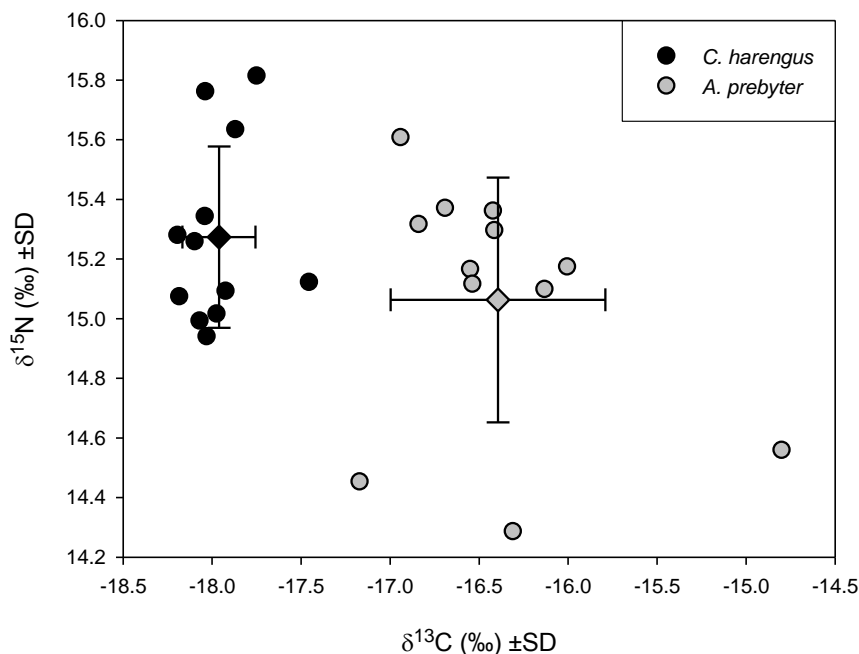


Fig. 6.3 Isotopic signatures of carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) for *Clupea harengus* and *Atherina presbyter* in per mill (‰). Diamonds represent mean values with standard deviation.

Herring ( $-18.0 \pm 0.2$ ) was significantly ( $p < 0.05$ ) depleted in  $\delta^{13}\text{C}$  compared to sand smelt ( $-16.4 \pm 0.6$ ) (Fig. 6.3). No significant difference was found between the mean  $\delta^{15}\text{N}$  of herring ( $15.3 \pm 0.3$ ) and sand smelt ( $15.1 \pm 0.4$ ).

In the mesocosm experiments herring and sand smelt showed significant differences in zooplankton predation rates. Although significant depletion in total zooplankton abundance in both herring and sand smelt mesocosms was found after 72 hours (Fig. 6.4), significant differences in predation rates could be identified on the level of individual prey taxa. Compare to the controls, a significant decrease of balanid larvae (including cypris and nauplius larvae), calanoid copepods and gastropod larvae was found in the tanks with sand smelt after 72 hours (Fig. 6.5). For the tanks with herring significant depletion was found only for calanoid copepods. Mainly calanoid copepods (80.8%) were found in the guts of herring at the end of the first set of experiments (Fig. 6.6). The guts of sand smelt were filled with barnacle cypris larvae (64.1%) and harpacticoid copepods (30%). After the second set of experiments guts of both species were full of harpacticoid copepods.

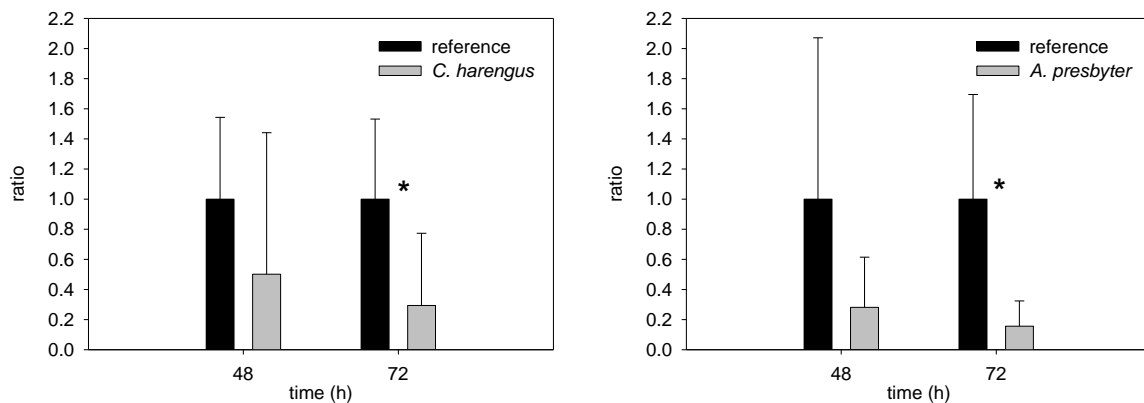


Fig. 6.4 Ratio with standard deviation of total zooplankton abundance between reference tanks and tanks with fish. Significant differences ( $p < 0.05$ ) between reference mesocosms and mesocosms with fish are marked with an asterisk.

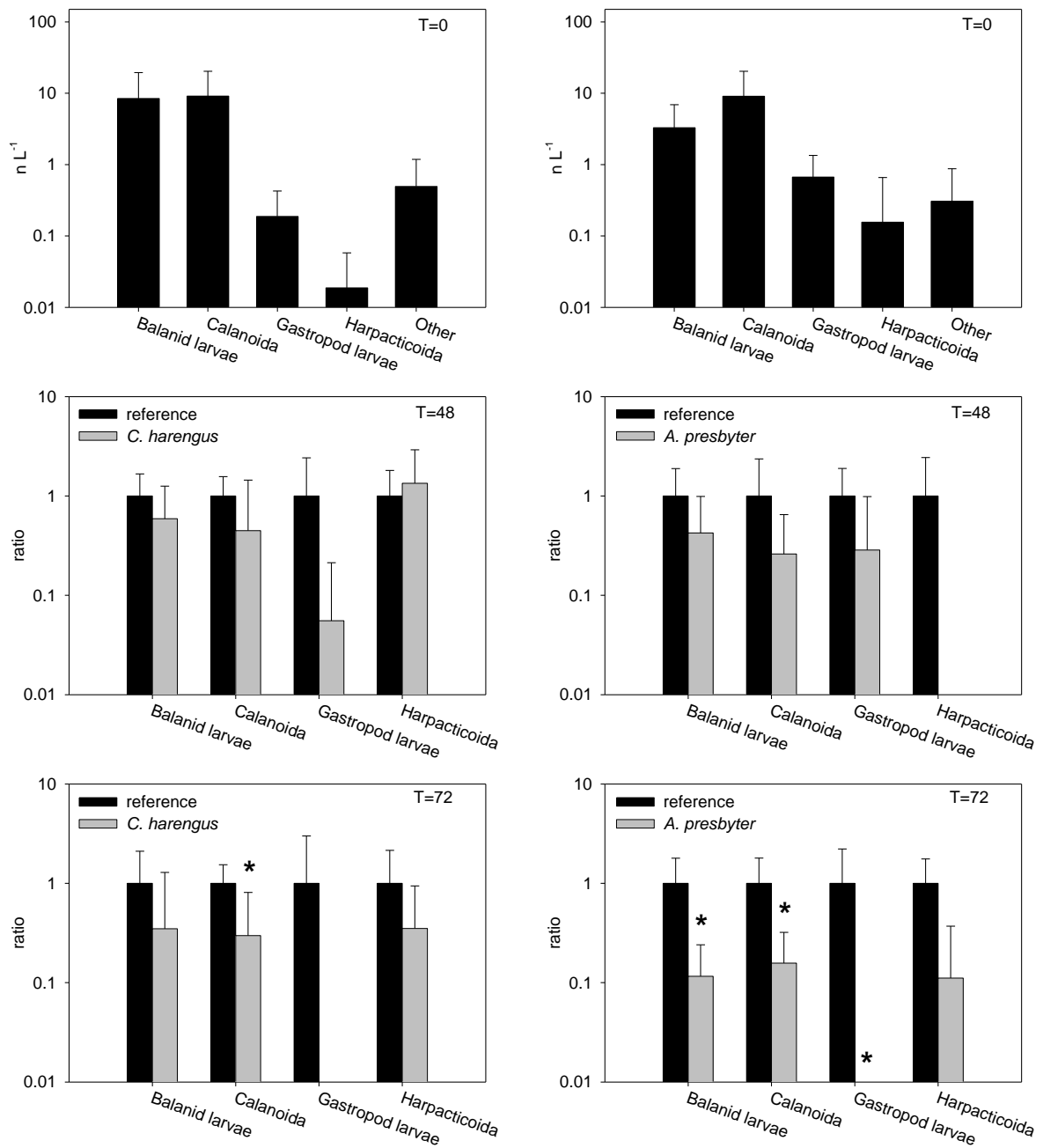


Fig. 6.5 Zooplankton abundance in individuals per liter ( $n L^{-1}$ ) with standard deviation in mesocosms at the beginning of the experiment (T=0) and ratio between average reference and tanks with fish after 48 hours (T=48) and after 72 hours (T=72). Significant differences ( $p < 0.05$ ) between reference tanks and tanks with fish are marked with an asterisk. Please note logarithmic y-axis.

Tab. 6.3 Intraspecific (Wallace and Ramsey 1983) and interspecific diet overlaps of *Clupea harengus* and *Atherina presbyter* calculated by Pianka's niche overlap index.

		intraspecific diet overlap				Interspecific diet overlap
		<i>C. harengus</i>		<i>A. presbyter</i>		
		mean	range	mean	range	
2006	August	0.87	0.55-1	0.99	0.97-1	0.41
	September	0.91	0.79-0.97	1	1	0.97
2008	August	0.97	0.87-1	0.82	0.40-0.96	0.99
	September	0.97	0.97-0.98	0.97	0.90-1	0.14
2010	September	0.91	0.86-0.95	0.98	0.95-1	0.26

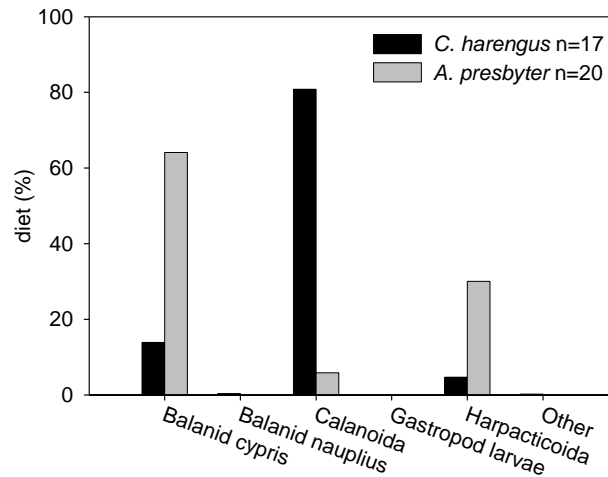


Fig. 6.6 Prey taxa found in the guts of *Clupea harengus* and *Atherina presbyter* at the end of the first set of experiments in percentage (%) of diet composition.

## 6.4. Discussion

### 6.4.1 Diet composition

Both herring and sand smelt fed almost exclusively on zooplankton. For herring these results were expected and are in accordance with other studies analyzing diets of herring of similar size classes (Sandström 1980, Last 1987, Arrhenius 1996, Kellnreitner et al. 2011) and most of these studies found copepods as main dietary component. Studies on



the diet of sand smelt showed a high amount of benthic invertebrates in the diet of sand smelt in estuarine environments (Pombo et al. 2002, 2005). In marine environments copepods dominated (Kislalioglu and Gibson 1977, Moreno and Castro 1995) although Turnpenny et al. (1981) stated that in larger (10.4 cm) individuals more macrofaunal prey was found than in smaller fish. This high amount of zooplankton prey consumed by fish < 10 cm is consistent with our results but the high amount of larval barnacles in the diet of sand smelt was to our knowledge not documented before and might hint on an exceptional high production of meroplankton in the area and a potential source for niche partitioning of planktivorous fish.

#### 6.4.2 Selection of prey

Certainly, the differing diets of herring and sand smelt are reflected in the selection index. Nevertheless, additional conclusions can be drawn from the results. They indicate that the diet differences among species are not a result of herring selecting calanoid copepods but rather of sand smelt avoiding such. Sand smelt selected calanoid copepods only during August 2008, when zooplankton abundance was generally low. Correspondingly, herring fed on a high percentage on barnacle cypris larvae during September 2006, when lowest calanoid copepod abundance during the whole investigation was found. This indicates that both herring and sand smelt switched their prey preferences according to zooplankton densities in the environment.

Herring is known to adjust feeding behavior and select prey according to prey size (Sandström 1980, Gibson and Ezzi 1985), visibility (Checkley 1982) and particle concentration (Gibson and Ezzi 1985, 1990). Although we did not actually measure prey sizes in fish guts, literature data show differences in size between cypris and nauplii stages of barnacle larvae and adult stages of calanoid copepods present in the bight. While barnacle larvae of *A. modestus* are usually smaller than 0.55 mm (Luther 1987), the most abundant calanoid copepods of the bight in late summer and autumn, *Acartia tonsa* (Martens, unpubl. res.), grow up to 1.2 mm in body length (Berggreen et al. 1988). This would corroborate with the results from Sandström (1980) and Flinkmann (1992) found in the Baltic Sea where adult herring preferred larger individuals of a particular prey.

To our knowledge no studies on the prey selectivity of sand smelt are published but it is known to feed on prey of various size classes (Turnpenny et al. 1981, Pombo et al. 2005). Hence, differences in prey selection could be attributed to differences in the distribution of the individual prey taxa. Zooplankton undertakes diel vertical migrations

induced by light (Forward 1988). In an experiment by Crisp and Ritz (1973) cypris larvae displayed low photokinesis, whereas positive phototaxis was shown for *Acartia tonsa* (Stearns and Forward 1984). Therefore, cypris larvae could be more evenly distributed in the water column, while copepods were closer to the surface. On sunny days during our samplings we could frequently observe juvenile herring feeding close to the water surface by particulate feeding. It is likely that calanoid copepods were well visible for herring against the bright surface. This behavior was already observed by Batty et al. (1990). As we could not observe this behavior for the sand smelt, differences in selectivity could result from feeding in a different depth zones. Nevertheless, to validate these assumptions vertically resolved zooplankton surveys will be necessary.

#### 6.4.3 Stable isotope analysis

In marine coastal environments enrichment in  $\delta^{13}\text{C}$  values of consumers indicate a benthic origin of prey (France 1995). The higher  $\delta^{13}\text{C}$  values found for sand smelt compared to herring could therefore suggest that higher proportion of benthic prey is consumed by sand smelt although we found none in the gut content analysis. It is possible that barnacle larvae were more enriched in  $\delta^{13}\text{C}$  than calanoid copepods, but this remains to be proved. Moreover, high  $\delta^{13}\text{C}$  values were found for fish feeding in intertidal areas (Kellnreitner unpubl. res.), which is the preferred habitat of sand smelt in the Sylt-Rømø bight (Kellnreitner et al. 2011). Similar isotopic composition of nitrogen in the tissues of both species indicates that they fed at a similar trophic position. This is consistent with gut content analysis as we found mainly herbivorous zooplankton in the diets of both species. Nevertheless, stable isotope composition indicates that differences in the feeding habits between the two species are prevailing as it reflects nutrition of the last 2-4 months (Pinnegar and Polunin 1999).

#### 6.4.4 Mesocosm experiment

The diet analysis at the end of the first experiment confirms the results obtained in the field. Sand smelt did prefer barnacle larvae and herring calanoid copepods also in the experimental setup. The high amount of harpacticoid copepods found in the guts after the second experiment was most likely an experimental artifact. Strong easterly winds during the last days of the experiment may have resuspended benthic harpacticoid copepods (Martens 1980) which then have entered the water circuit and could have passed through the filter mesh because of their smaller size. The total plankton abundance at the end of the second experiment was also very low and fish could have searched for alternative food sources close to the bottom of the tanks were harpacticoid

copepods accumulated. Additionally, tank effects such as the rate of water exchange, turbulence and temperature fluctuations (Howarth et al. 1993, Notini et al. 1977), wall effects (Lundgren 1985), lack of predators and spatial scaling (Schindler 1998) have to be taken into account when interpreting mesocosm experiments.

#### 6.4.5 Is sand smelt establishment promoted by *Austrominius modestus*?

Due to the high ingestion of cypris larvae by the sand smelt, the question arises if *Austrominius (Elminius) modestus* promotes the establishment of the sand smelt in the northern Wadden Sea. Originating from southern Australia and New Zealand, *A. modestus* was introduced to the North Sea region in the first half of the 20<sup>th</sup> century (Crisp 1958). The recent increase *A. modestus* in the Sylt-Rømø Bight is related to climate warming and most recently *A. modestus* dominated barnacle assemblages of the Sylt-Rømø Bight (Witte et al. 2010). The main settling period of this barnacle species is in August and September (Luther 1987, Harms and Anger 1983) and we therefore assume that the bulk of barnacle larvae in our samples were *A. modestus*. Because native barnacles of the Sylt-Rømø Bight have their main reproduction period in spring and have only a minor reproduction event in summer or late summer, brood waves of *A. modestus* could be an important food source for the sand smelt in this region. Since species identification of cypris larvae found in the guts by morphological methods revealed to be problematic, molecular methods should be employed in further studies to validate these assumptions (Symondson 2002).

#### 6.4.6 Competition between herring and sand smelt?

Both species showed opportunistic feeding behavior and a shift in selection towards abundant prey when preferred prey became limited. Occasionally this resulted in high food overlap but most of the time overlap was low. Nevertheless, competition between the two species could potentially occur should their zooplankton resources become limited. However, it was observed that sand smelt showed slightly different distribution patterns than herring within the Sylt-Rømø tidal basin. Results of Kellnreitner et al. (2011) revealed that sand smelt distribution was limited to the littoral zone, while herring was also abundant in the deeper parts of the bight. Thus, sand smelt occupies only a fraction of the herring habitat. From our results we conclude that an increase in sand smelt population should not interfere with the nursery function of the Wadden Sea for herring. Absent or very rare in the northern Wadden Sea before, the sand smelt became established in this area integrated into the systems food web without apparent effects on foraging herring.

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## 7. General Discussion

Coastal management of living resources focuses more and more on a regional environmental scale (Pasquaud et al. 2007). The importance of research on ecosystem level is therefore high. Elton (1927) stated that the main ecological process connecting organisms is their feeding relations. While classification into general feeding modes only allows comparisons between different regions or habitats, the study of feeding interactions requires calculation of diet overlaps which in their turn need more detailed data. Only analyses of individuals caught at the same location and during the same time period permit to draw conclusions on direct feeding interactions and competition, both on community level and between two distinct species.

The first two studies (chapter 3 and 4) represent the base for the analysis of feeding interactions of native fish with alien species. The sea walnut (*Mnemiopsis leidyi*) and the sand smelt (*Atherina presbyter*) are two new species in the food web of the Sylt-Rømø Bight. The trophic interactions between both species and native fish were subject of the second part of the thesis (chapter 5 and 6). Most interactions of both the sea walnut and the sand smelt were assumed to occur with the zooplanktivorous feeding guild. We chose juvenile herring (*Clupea harengus*) as representative of native zooplanktivorous fish because of its dominance in the catches and its commercial importance (Simmonds 2007). Furthermore, juvenile herring were easily accessible for the experiments and practical to keep in mesocosms. Conclusions resulting from this second part apply primarily to zooplankton feeding fish. Nevertheless, the results of the first two studies deliver an array of new information, which will help to fill the gaps of the present Sylt-Rømø Bight food web model.

### 7.1. The present state of the fish food web of the Sylt-Rømø Bight

The high spatial and time resolution of stomach content analysis of the whole fish community was never realized in the Wadden Sea before although it is crucial for the precise description of fish diets in such a variable environment. Most of the fish showed opportunistic feeding behavior and adapted to abundant prey (chapter 3). The high time resolution accounted for the variability in prey and reduced the bias normally caused by

this variation. Additional information on trophic positions was gained through the stable isotope analysis (chapter 4). The results were on average slightly higher than results found by Baird et al. (2004) for trophic position of 7 fish species calculated by network analysis. Comparison of results from gut content analysis reveals different prey items where differences between trophic positions were highest. Microplankton food chains were perhaps overlooked, explaining lower trophic position of zooplanktivorous fish in Baird et al. (2004). The combination of gut content and stable isotope analysis yields insights into provenance of food, trophic positions and importance of prey items (Fig. 7.1).

Results show large differences in the abundance and species composition of the fish community between intertidal and subtidal areas of the Wadden Sea. The intertidal area is the best described part of the Sylt-Rømø Bight (Baird et al. 2004, 2007). Gobies dominate this area in abundance. The most abundant of all is the common goby (*Pomatoschistus microps*). They inhabit mainly the bare sand flats and seagrass meadows around mean tide level (Polte and Asmus 2006). These parts represent the major fraction of the intertidal area and are almost free of alien species (Nehring et al. 2011). Therefore, the intertidal area underwent only minor changes regarding fish species composition compared to the 1990s (Herrmann et al. 1998) or even earlier times (Dunker and Ladiges 1960, Wohlenberg 1935). An exception is the sand smelt, which is found in larger numbers than ever before and seems to reproduce in the intertidal seagrass meadows (Polte and Asmus 2006). Changes might also have occurred on the newly developed mixed oyster/mussel beds. These areas require considerable and elaborated sampling effort and were not investigated during this thesis. Nevertheless, they form a highly structured habitat which accumulates organic material (Kochmann et al. 2008) creating an important feeding habitat for mobile species (Coen et al. 2007).

But also fish themselves act as important accumulator and vector of organic matter and energy (eg. Deegan 1993). In this context large differences in the origin of transported organic matter between the different feeding guilds of fish found in this study exist. The bulk of zooplanktivorous species in this study are migrating fish covering large distances during their ontogeny as well as short distances with changing of tides. These are mostly highly mobile species occurring in various depth and habitats within the Wadden Sea. Most abundant species were herring and sand lance (*Ammodytes tobianus*). The base of their diet is phytoplankton and both species are an important food source for piscivorous fish and birds (Dähnhardt et al. 2011). Zooplanktivorous fish channel the primary production of the water column towards higher trophic levels. The zoobenthivorous feeding guilds comprise more territorial fish species than the zooplanktivorous feeding

guilds. Transport of organic matter and energy by zoobenthivorous fish covers shorter distances than in zooplanktivorous fish. The highest amount of energy within the bight is transported by *P. microps*. It feeds at high tide on intertidal areas with microphytobenthos as base of its diet. Through *P. microps* a part of the primary production of the intertidal area is exported and made available for higher trophic levels (Behrends 1985, Pockberger et al. submitted).

A higher abundance of Lusitanian fish species was found than in previous studies (Baird et al. 2004, 2007, Herrmann et al. 1998). This increase is most likely caused by rising temperatures due to climate change (Rose 2005, Walther et al. 2002). Wiltshire and Manly (2004) found a temperature increase of 1.13°C between 1962 and 2002 and temperature data from Martens and Beusekom (2008) show a prolonged summer period with significantly higher September temperatures in the 2000s than before. Rose (2005) concluded that fish species preferring cooler water temperatures may shift northwards when temperatures rise. Until now we could not find clear differences in the occurrence of boreal species in the Sylt-Rømø Bight between the previous studies and our results, although short-term effects of high summer water temperatures on eel pout were observed.

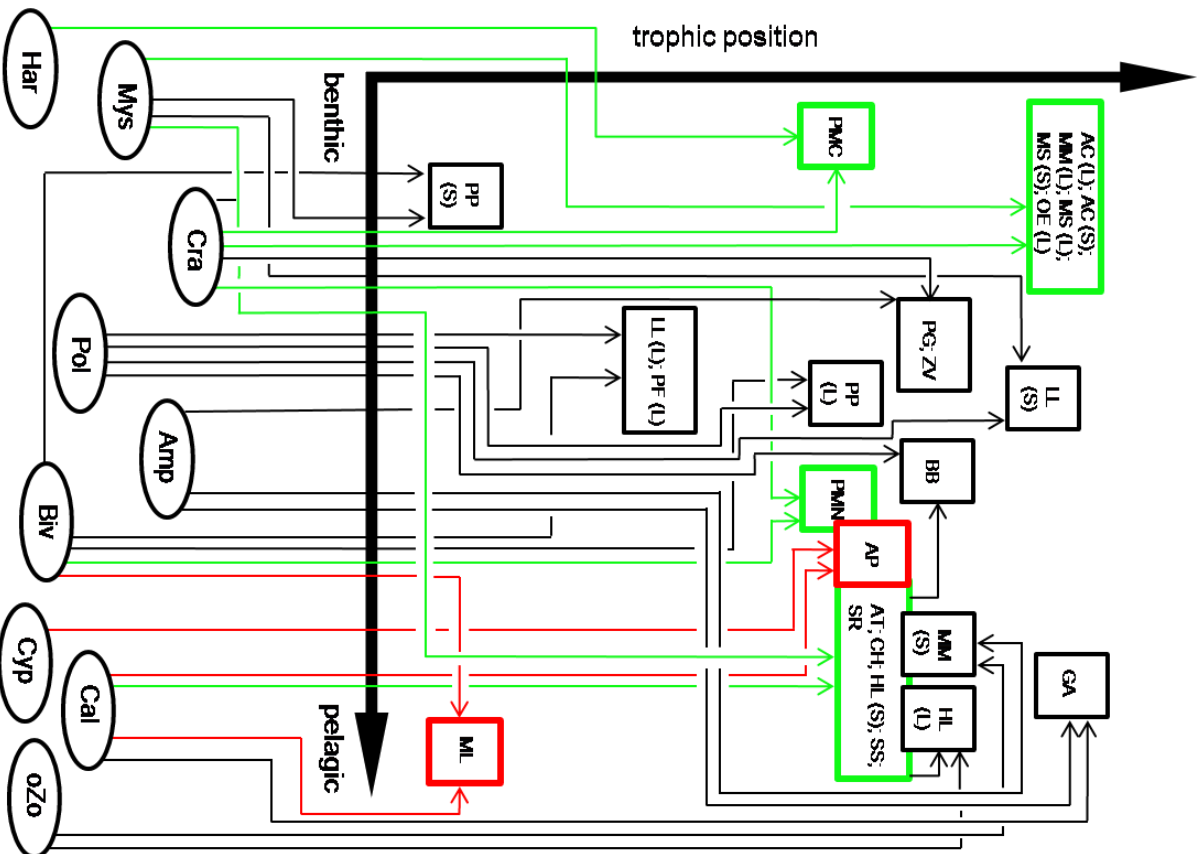


Fig. 7.1 Schema of the fish food web of the Sylt-Rømø Bight showing fish species grouped into feeding guilds whenever possible and the prey organisms dominating their diet. Stable isotope analysis was used to infer trophic position and provenance of food, and gut content analysis to determine dominant prey. In green colour – most abundant guilds and species; in red colour – the new species in the Sylt-Rømø food web; AC – *Agonus cataphractus*, AP – *Atherina presbyter*, AT – *Ammodytes tobianus*, CH – *Clupea harengus*, BB – *Belone belone*, GA – *Gasterosteus aculeatus*, HL – *Hyperoplus lanceolatus*, LL – *Limanda limanda*, ML – *Merluccius leucostictus*, MM – *Merlangius merlangus*, MS – *Myoxocephalus scorpius*, OE – *Osmerus eperlanus*, PF – *Platichthys flesus*, PG – *Pholis gunnellus*, PMC – *Pomatoschistus microps*, PMN – *Pomatoschistus minutus*, PP – *Pleuronectes platessa*, SS – *Sprattus sprattus*, SR – *Syngnathus rostellatus*, ZV – *Zoarces viviparus*, Amp – Amphipoda, Biv – Bivalvia, Cal – Calanoida, Cra – *Crangon crangon*, Cyp – Cypris, Har – Harpacticoida, Mys – Mysidacea, ozo – other zooplankton, Pol – Polychaeta;

It is worth noting that a higher proportion of zooplanktivorous fish was found in this study than in the investigation by Herrmann et al. (1998). This could be a result of the large inter-annual variation in fish abundance and species composition encountered in the region (Herrmann et al. 1998), but may also follow trans-regional trends (Jennings et al. 2002, Pauly et al. 1998). The highest trophic positions in the Wadden Sea fish food web are occupied by demersal and benthic fish species. These fish species are under a high fishing pressure, either as target species or as by-catch in the brown shrimp (*Crangon crangon*) fishery (Suuronen and Sardà 2007). Changes in the upper trophic levels may entail modifications in the whole food web of the Wadden Sea through loss of top down control and cascading effects (Heithaus et al. 2008, Stevens et al. 2000). The dramatic decline of diadromous and large benthic predatory fish (Tab. 7.1) due to overexploitation in the beginning of the last century surely involved such changes in the food web. This effect has been described by Duffy (2003) as “trophic skew” and was investigated by Byrnes et al. (2007). The latter found that extinction or loss of species in a system occurred predominantly in higher trophic levels. New species entering the system through invasions or migration were mainly filter feeders and planktivores of lower trophic level. These changes in the trophic pyramid might lead to changes in production, total biomass, top-down/bottom-up control and other important ecosystem level processes (Byrnes et al. 2007, Duffy 2003, Duffy and Stachowicz 2006, Lotze 2005 and references therein). A first step in the understanding of the change in these processes will be the evaluation of the role of the new species in the affected areas.

Tab. 7.1 Fish species occurring in the Wadden Sea. From Witte and Zijlstra 1979 (a), Vorberg and Breckling 1999 (b), Hinz 1989 (c), Herrmann et al. 1998 (d), this study 2011(e). xx – common, x – present, o – extremely rare, \* - common before 1940, ? - presence not validated; No information on abundance is given for Hinz (1989), Vorberg and Breckling (1999). Information from Herrmann et al. (1998) only distinguish between present and rare.

Scientific name	Common names		STUDY				
	English	German	a	b	c	d	e
			LOCATION	German WaddenSea	Nothern WaddenSea	Trischen-Elb-mündung	SRB
Years sampled			1931-1978	1988-1995	1986, 1987	1993-1995	2008-2010
<i>Acipenser sturio</i>	Sturgeon	Stör	x				
<i>Agonus cataphractus</i>	Hook-nose	Steinpicker	xx	x	x	x	xx
<i>Alosa alosa</i>	Allis shad	Maifisch	o				
<i>Alosa fallax</i>	Twaite shad	Finte	xx	x		o	o
<i>Ammodytes marinus</i>	Lesser sand-eel	Kleiner Sandaal				x	
<i>Ammodytes tobianus</i>	Small sand-eel	Kleiner Sandaal	xx	x	x	x	xx
<i>Anguilla anguilla</i>	Eel	Aal	xx	x	x	x	x
<i>Aphia minuta</i>	Transparent goby	Glasgrundel	o	x		x	o
<i>Arnoglossus laterna</i>	Scaldfish	Lammzunge	o				
<i>Atherina presbyter</i>	Sand smelt	Ährenfisch		x		o	x
<i>Belone belone</i>	Garfish	Hornhecht	xx	x	x	o	x
<i>Buglossidium luteum</i>	Solenette	Zwergzunge	xx	x	x	x	
<i>Callionymus lyra</i>	Dragonet	Gestreifter Leierfisch	xx	x	x	x	o
<i>Callionymus maculatus</i>	Reticulated dragonet	Gefleckter Leierfisch		x			
<i>Chelon labrosus</i>	Thick-lipped mullet	Dicklippige Meeräsche	xx	x	x	o	x
<i>Ciliata mustela</i>	Five-bearded rockling	Fünfbärtelige Seequappe	xx	x	x	x	x
<i>Clupea harengus</i>	Herring	Hering	xx	x	x	x	xx
<i>Conger conger</i>	Conger eel	Meeraal	x				
<i>Coregonus lavaretus oxyrhynchus</i>	Houting	Nordseeschnepel	*/o	x		o	
<i>Ctenolabrus rupestris</i>	Gold sinny	Klippenbarsch	o				
<i>Cyclopterus lumpus</i>	Lumpsucker	Seehase	x	x	x	x	x
<i>Dasyatis pastinacia</i>	Sing ray	Stechrochen	xx				
<i>Dicentrarchus labrax</i>	Sea bass	Seebarsch	x				o
<i>Engraulis encrasicolus</i>	Anchovy	Sardelle	x/xx	x		o	x
<i>Entelurus aequoreus</i>	Snake pipefish	Schlangennadel	x	x		o	o
<i>Eutriglia gurnardus</i>	Grey gurnard	Grauer Knurrhahn	xx	x		o	
<i>Gadus morhua</i>	Cod	Dorsch	xx	x	x	x	x
<i>Gaidropsarus mediterraneus</i>	Shore rockling	Mittelmeer Seequappe		x			
<i>Galeorhinus galeus</i>	Tope	Hundshai	?	x			
<i>Gasterosteus aculeatus</i>	Stickleback	Dreistacheliger Stichling	xx	x	x	x	xx
<i>Glyptocephalus cynoglossus</i>	Witch flounder	Zungenbutt		x			
<i>Hyperoplus lanceolatus</i>	Greater sandeel	Schnauzenfleck Sandaal	x	x		x	xx
<i>Labrus bergylta</i>	Ballan wrasse	Gefleckter Lippfisch	o				
<i>Lamna nasus</i>	Porbeagle	Heringshai	o				
<i>Lampetra fluviatilis</i>	Lampern	Flussneunauge	xx	x	x	o	x
<i>Limanda limanda</i>	Dab	Kliesche	xx	x	x	x	xx
<i>Liparis liparis</i>	Sea snail	Großer Scheibenbauch	xx	x	x	x	x



Tab. 7.1 continued

scientific name	common names		a	b	c	d	e
	English	German					
<i>Liparis montagui</i>	Montagus seasnail	KleinerScheibenbauch		x			
<i>Liza ramada</i>	Thin-lipped mullet	Dünnlippige Meeräsche	x				
<i>Maurolicus muelleri</i>	Pearl-side	Leuchtsardine		x		o	
<i>Merlangius merlangus</i>	Whiting	Wittling	xx	x	x	x	xx
<i>Microstomus kitt</i>	Lemon sole	Rotzunge	x	x		x	x
<i>Mola mola</i>	Sunfisch	Mondfisch	o				
<i>Molva molva</i>	Ling	Leng		x			
<i>Mullus surmuletus</i>	Red mullet	Streifenbarbe		x		o	x
<i>Myoxocephalus scorpius</i>	Bull rout	Seeskorpion	xx	x	x	x	xx
<i>Osmerus eperlanus</i>	Smelt	Stint	xx	x	x	x	xx
<i>Petromyzon marinus</i>	Sea lamprey	Meerneunauge	x	x			
<i>Pholis gunnellus</i>	Butter fish	Butterfisch	xx	x	x	x	xx
<i>Platichthys flesus</i>	Flounder	Flunder	xx	x	x	x	xx
<i>Pleuronectes platessa</i>	Plaice	Scholle	xx	x	x	x	xx
<i>Pollachius virens</i>	Saithe	Köhler	x	x		o	o
<i>Pomatoschistus lozanoi</i>	Lozano's goby	Lozanos Grundel	?	?		?	x
<i>Pomatoschistus microps</i>	Common goby	Strandgrundel	xx	x	x	x	xx
<i>Pomatoschistus minutus</i>	Sand goby	Sandgrundel	xx	x	x	x	xx
<i>Pomatoschistus pictus</i>	Painted goby	Fleckengrundel		x			o
<i>Psetta maxima</i>	Turbot	Steinbutt	xx	x	x	o	o
<i>Pungitius pungitius</i>	Ten-spined stickleback	Neunstacheliger Stichling		x			o
<i>Raja clavata</i>	Thornback	Nagelrochen	*				
<i>Raniceps raninus</i>	Tadpole-fish	Froschdorsch	o				
<i>Rhinonemus cimbricus</i>	Four-bearded rockling	Vierbärtelige Seequappe	o	x			
<i>Salmo salar</i>	Salmon	Lachs	x	x			?
<i>Salmo trutta</i>	Sea trout	Meerforelle	xx	x	x	o	o
<i>Sardinapilchardus</i>	Pilchard	Sardine		x			
<i>Scomber scombrus</i>	Atlantic mackerel	Atlantische Makrele	xx	x		o	x
<i>Scophthalmus rhombus</i>	Brill	Glattbutt	xx	x	x	o	o
<i>Scyliorhinus caniculus</i>	Dog fish	Kleiner Katzenhai	o				
<i>Solea solea</i>	Sole	Seezunge	xx	x	x	x	x
<i>Spinachia spinachia</i>	Sea stickleback	Seestichling	x	x		x	x
<i>Sprattus sprattus</i>	Sprat	Sprotte	xx	x	x	x	xx
<i>Squalus acanthias</i>	Spur-dog	Dornhai	o				
<i>Syngnathus acus</i>	Greater pipefish	Große Seenadel		x		x	
<i>Syngnathus rostellatus</i>	Nilsson's pipefish	Kleine Seenadel	xx	x	x	x	xx
<i>Syngnathus typhle</i>	Deep-snouted pipefish	Grasnadel	*				
<i>Taurulus bubalis</i>	Sea skorpion	Seebull	x	x		o	
<i>Trachinus vipera</i>	Lesser weever	Kleiner Petermann	o				
<i>Trachurus trachurus</i>	Scad	Stöcker	xx	x	x	x	x
<i>Triglia lucerna</i>	Tub gurnard	Roter Knurrhahn	x	x		o	x
<i>Trisopterus esmarkii</i>	Norway pout	Stintdorsch		x			
<i>Trisopterus luscus</i>	Bib	Franzosendorsch	xx	x	x	x	o
<i>Trisopterus minutus</i>	Poor-cod	Zwergdorsch	o	x			
<i>Xiphiasgladius</i>	Sword-fish	Schwertfisch	o				
<i>Zeugopterus punctatus</i>	Top knot	Haarbutt			x		
<i>Zeus faber</i>	Dory	Heringskönig	o				
<i>Zoarces viviparus</i>	Eel pout	Aalmutter	xx	x	x	x	xx

## 7.2. Alien species in the Wadden Sea fish food web

Alpert (2006) stated that more diverse communities are less invasible. The Wadden Sea is a comparatively young system and offers still resources and niches for newly arriving species (Reise 2010). It is situated in an important economic zone and the proximity to large ports as Hamburg, Bremerhaven and Amsterdam facilitate introductions via ballast water (Firestone and Corbett 2005, Williams et al. 1988). Nevertheless, moderate amounts of alien species are observed in the Wadden Sea (52 species) (Reise et al. 2002) compared to other coastal ecosystems as Chesapeake Bay (116 species) and San Francisco Bay (212 species) (Ruiz et al. 1997).

Once an introduced species is established in the Wadden Sea area they inevitably become part of the food web. The involved changes can have detrimental or beneficial effects for the Wadden Sea fish. Predation on native fish by introduced species in the Wadden Sea has to our knowledge never been reported, nor could we observe it in the area of the Sylt-Rømø Bight. Theoretically, predation of sea walnut on fish eggs and larvae is possible (Shiganova and Bulgakova 2000), but at least in the Wadden Sea temporal overlap between the occurrence of pelagic fish eggs and larvae and sea walnut blooms is low (see also Riisgård et al. 2011). We demonstrated that competition of alien species with native fish is possible. Although we did not demonstrate effects of competition in natural fish assemblages, we hypothesize that due to the temporarily high food overlap competition is likely, should zooplankton resources be limited. Moreover, the high amount of introduced suspension feeders could entail cascading trophic effects causing changes in zooplankton production (Polis and Holt 1992).

We found seven alien species (Tab. 7.2) in the diets of fish and it is likely that there were more. Several introduced polychaetes and crustaceans are abundant in the Sylt-Rømø Bight but identification to species level in fish gut contents was mostly not possible. Some of the introduced species were the dominant prey of the native fish. The razor clam *Ensis directus* was commonly used by flatfish (*L. limanda*, *P. flesus*, and *P. platessa*) and *Acartia tonsa*, a calanoid copepod, was the most abundant prey of zooplanktivorous fish in summer. These changes in the food web structure could have direct effects on predator abundances and also entail cascading effects on higher and lower trophic levels (Menge 1995, White et al. 2006). The effects of such changes are best revealed by models like Network analysis (Ulanowic and Kay 1991) or experimental approaches (Menge 1997). The goal of the methods employed in this study was a high resolution in the identification of diets. The consequential diet overlaps are the first step

in evaluating the potential for competition not only between native but also between native and alien species.

Until now, no extinctions due to alien species in the Wadden Sea are documented. Extinction of a native species through competition with an alien species is rare (Davis 2003). Nevertheless competition could be an important factor controlling invasive species. Release from competition, as assumed by Bilio and Niermann (2004) for the sea walnut in the Black Sea, leaves more resources for the introduced species and is beneficial for its propagation.

Tab. 7.2 Introduced species found in the diets of fish in the Sylt-Rømø Bight.

Prey taxon	Ontogenetic stage
<b>Bivalvia</b>	
<i>Crassostrea gigas</i>	larvae?
<i>Ensis americanus</i>	larvae?, juvenile, adult
<i>Mya arenaria</i>	larvae?, juvenile, adult
<b>Gastropoda</b>	
<i>Crepidula fornicata</i>	juvenile
<b>Crustacea</b>	
<i>Acartia tonsa</i>	larvae, juvenile, adult
<i>Austrominius modestus</i>	larvae?
<i>Caprellamutica</i>	adult

### 7.3. "Invasiveness" of *Atherina presbyter* and *Mnemiopsis leidyi*

We investigated the feeding interactions of juvenile herring with two relatively new species in the system of the Sylt-Rømø Bight (chapter 5 and 6). Both species overlap in their diet to a certain extent with juvenile herring. Interestingly both species switch to a meroplankton prey while herring keeps feeding on copepods. Nevertheless, most of the time diet overlap with herring was high. It is worth noting, that the bulk of meroplankton species in the diet are likely larvae from other introduced species. Identification of these organisms was not realized due to the difficulties to discern the larvae morphologically from larvae of native species. However, based on timing of reproduction we estimate the major proportion being the barnacle *Austrominius modestus* and pacific oyster *Crassostrea gigas*.

From our results we infer that sand smelt and sea walnut might strongly differ in their ability to integrate into the Sylt-Rømø Bight food web. While both species are feeding on zooplankton, they show important differences in their biology. Most important are the differences in their distribution, ontogeny and reproduction. The sand smelt is an active swimmer and mostly remains close to the coast, while the sea walnut is primarily distributed by currents and wind and therefore unevenly distributed over the total bight (Fig. 7.2). In the Sylt-Rømø Bight the sand smelt occupies a habitat which is only occasionally visited by herring and native zooplanktivorous fish in general, but all zooplanktivorous fish in the bight share their distribution range with the sea walnut (Fig. 7.2). Reproduction of sand smelt in the seagrass meadows of the bight is likely to occur in summer (Bamber et al. 1985, P. Polte and Asmus 2006) and eggs, larvae and juveniles might be a food source for several native species. The size at maturity is about 7 to 8 cm and therefore young of the year reproduce only in the summer of the next year (Moreno et al. 2005, Turnpenny et al. 1981). We assume that, stock size is mainly depending on the amount of sand smelts entering the bight in summer and on favourable environmental conditions, particularly for recruits in the first weeks after hatching. In contrast, the sea walnut is a hermaphrodite reproducing in the water column (Kremer 1976). Considering the high growth rates (Reeve et al. 1989) and the low size at first maturity (Finenko et al. 2006) the new generation is most likely already able to reproduce in their first season. The size of the bloom is therefore mostly dependent on the environmental conditions the sea walnut encounters in the bight.

We found no predators of sea walnut in higher abundance during our samplings. Possible predators like lump sucker (*Cyclopterus lumpus*), smelt (*Osmerus eperlanus*) and the ctenophore *Beroe* sp. were found in low abundance and mostly not in the same time period as sea walnut. As in many other marine ecosystems comb jelly fish and jelly fish in general represent a trophic dead end in the food web as their high water content and therefore low nutritional value makes them an undesirable prey for most higher trophic level consumers (Sommer et al. 2002). Jelly fish have been reported to release large quantities of carbon rich DOM which was quickly metabolized by bacterioplankton (Condon et al. 2011). The strengthening of the microbial food web in return favours blooms of jelly fish through food supply to their favoured prey (Condon et al. 2011, Sommer et al. 2002). The apprehension arises, that once fully established the “jelly food chain” may represent an alternative stable status of the food web (Condon et al. 2011, Richardson et al. 2009, Sommer et al. 2002).

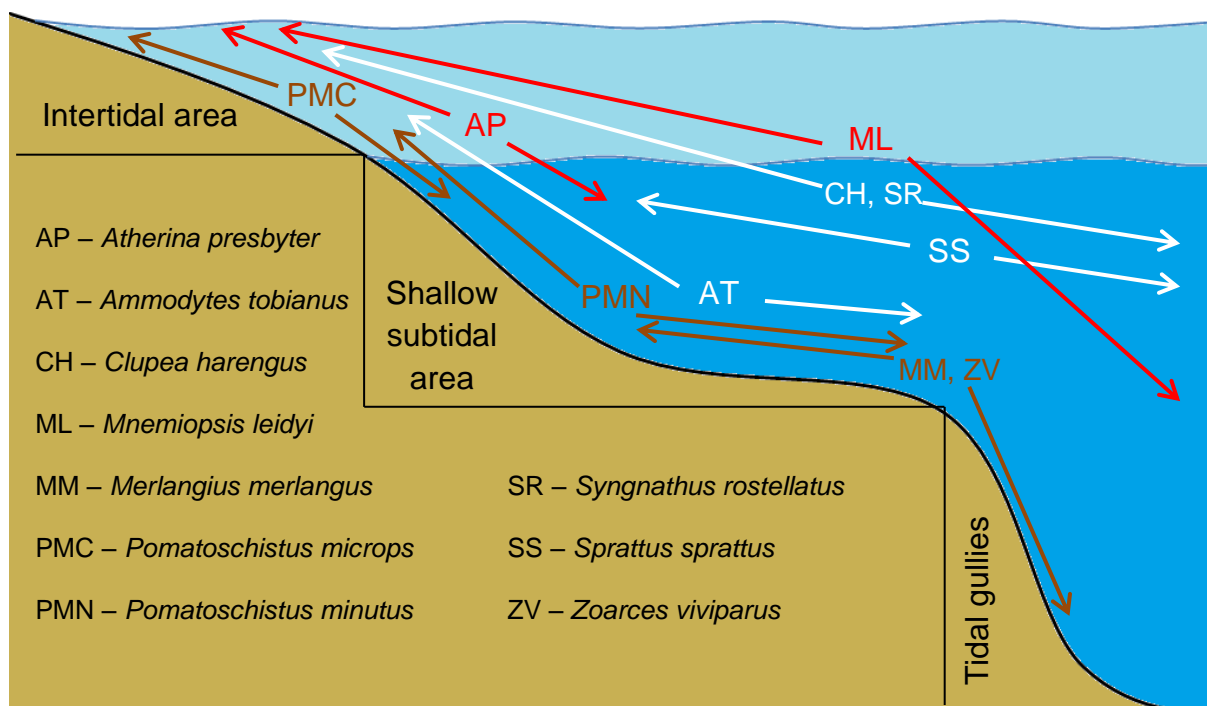


Fig. 7.2 Schema of the distribution of the four most abundant pelagic (in white) and benthic/demersal (in brown) fish species in the water column. New species in red.

The sand smelt in return, will possibly integrate into the food web of the Sylt-Rømø Bight. Although it shows high zooplankton grazing efficiencies and partly high food overlap with zooplanktivorous fish, it could be limited by the amount of suitable habitats in the bight. In the food web sand smelt occupies a similar niche like herring (Moreno and Castro 1995, Pinnegar and Polunin 2000) but using only small parts of the same habitat.

Both, sand smelt and sea walnut cannot be considered as fully established in the northern Wadden Sea as they both disappear in winter. In fact they show the same pattern as most of the native species in the Wadden Sea and use this ecosystem during times of favourable conditions. With some exceptions (eg. *Zoarces viviparus*, *Myoxocephalus scorpius*) most native Wadden Sea fish species immigrate into the North Sea during winter and it seems that sea walnut distribution follows a similar pattern as it is observed in low densities during winter at Helgoland (Boersma et al. 2007), but is missing in the Wadden Sea. The winter refuge and provenance of sand smelt entering the Sylt-Rømø Bight are still unknown and should be the question of further research.

#### 7.4. Critical review of the methods

Due to the high temporal resolution and the high number of sampling stations, sampling with the bottom trawl net from the “FK Mya” was restricted to one tidal period per station and per month. Because fish retreat to subtidal areas and tidal gullies during low tide, the hours around low water were chosen. Differences in abundance between the tidal periods were shown by Herrmann et al. (1998) during a 24 hour sampling. Especially for pelagic fish higher abundance was found during high tide. This implies that abundance of zooplanktivorous fish during our sampling may be higher than estimated, as parts of the herring stock seem to undertake short migrations out of the bight during low tide.

Sampling of the intertidal area with the beach seine was, as a matter of fact, restricted to high tide. Therefore, the results from the two methods were not combined to calculate total biomass of fish in the Sylt-Rømø Bight as fish migration between the two areas is likely. The results give information about the utilisation of the two habitats by the different fish species and seasonal differences within the areas are revealed.

For the analysis of diets gut content and stable isotope techniques were applied. For the preservation of fish for gut content analysis we chose the use of a buffered 5% formalin seawater solution. This entails a change in weight and volume of the preserved organisms, especially of organisms with high water volume (Beers 1976). A shrinkage or dissolution of gelatinous zooplankton due to formalin may lead to an underrepresentation of such organisms in the diets. However, we could find several species of such organisms well preserved in the diets of fish, but underrepresentation due to volume loss might be possible.

Due to the high costs involved in analysis of many stable isotope samples, we restricted our analysis to carbon and nitrogen isotopes. When multiple possible sources of primary energy are present, the use of additional elements is advisable (Connolly et al. 2004, Dufour and Gerdaux 2001). Most of the fish in our study are restricted to the marine environment. Their possible sources of primary energy are limited and the two major ones are phytoplankton and microphytobenthos. Exceptions are migrating and diadromous fish like the three-spined stickleback (*Gasterosteus aculeatus*), which may also derive energy from riverine and terrestrial energy sources.

An additional method for analysis of diets is the use of fatty acids as trophic markers (Budge et al. 2006). It is based on the principle that fatty acids of prey are deposited in the predator in a predictable way with little modification (Budge et al. 2006). This method

is easy to use in short food chains, but becomes difficult in the presence of omnivory and higher trophic levels (Dalsgaard et al. 2003).

Mesocosm experiments provide the possibility to manipulate environmental factors in a limited water body with conditions close to nature (Odum 1984). Kraufvelin (1999) stated that replicability, repeatability and ecological realism (see Tab. 7.3 for definitions) are common problems in the interpretation of mesocosm experiments. Replicability and repeatability problems are likely to increase with increasing degree of complexity of the mesocosm system. As the mesocosm systems in our experiments represented relatively simple pelagic systems these problems should play a minor role. Ecological realism was affected due to several problems that could not be avoided. Herring and sand smelt are swarm forming species that are not evenly distributed in the bight. Average densities would have resulted in less than one individual per tank, so we had to choose a practicable density permitting natural swarming behaviour and also replication for analysis. Plankton was added to the tanks in consecutive events rather than in a constant flow. Additional effects affecting the ecological realism in mesocosms are differences in the rate of water exchange, turbulence and temperature fluctuations (Howarth et al. 1993, Notini et al. 1977), wall effects (Lundgren 1985), lack of predators and spatial scaling (Schindler 1998). All these effects have to be taken in consideration when drawing conclusions from mesocosm experiments. To support the interpretation parallel field observations accompanied all our experiments.

Tab. 7.3 Definitions of replicability, repeatability and ecological realism (from Giesy and Allred 1985)

<b>term</b>	<b>definition</b>
replicability	similarity of replicate experimental units of an experimental treatment at a given point in time and space
repeatability	similarity of responses in systems which are observed at different locations or points in time
ecological realism	similarity between artificial system and natural ecosystem

### 7.5. Perspective

This thesis deals with new species affecting the fish food web of the Wadden Sea. Some of them arrived by introductions others expand their distributional range due to global warming. The consequences for the Wadden Sea ecosystem are difficult to predict and should be further investigated.

Baird et al. (2004) as a result from their network analysis pointed to the immature status of the Sylt-Rømø Bight. Reise (2010) therefore states that the Wadden Sea offers still place for many new species and that new and introduced species may augment biodiversity in the Wadden Sea. This may be true from a local point of view but globally biodiversity in the oceans is decreasing (Sax and Gaines 2003) which may lead to a stability loss on a global scale (Beisel and Devin 2007, Worm et al. 2006). Habitat destruction, exploitation and pollution lead to decreases in native species and newly arriving species may benefit (Alpert 2006, Sax et al. 2007). The susceptibility of a region or ecosystem for invasions and the presence of introduced species should therefore play an important role in coastal and fisheries management. This includes development of strategies against further introductions and consideration of competition with alien species in calculation of total allowable catches (TACs) of native species.

### 7.6. Conclusion

Most of the fish inhabiting the Wadden Sea are able to thrive in a wide variety of environmental conditions. Their environment is characterised by a high degree of variation both in the abiotic components and in the living resources they rely on. As a consequence Wadden Sea fish accept a broad variety of prey and are mostly only restricted by their gape width. To unfavourable abiotic conditions they react with emigration into the North Sea. Documented extinctions of fish species in the Wadden Sea are either ascribed to habitat loss or overexploitation (Lotze 2005). Until now no extinctions of fish species due to invasive species are known in the Wadden Sea area. A likely reason is that the Wadden Sea is a comparatively young system. In the short time, on an evolutionary scale, since the last glacial period only limited complex species interactions had the time to evolve. There are still plenty of resources available and niches that can be formed by new arriving species (Reise 2010). Also trophic interactions between alien or new species develop as in the case of *A. modestus* and sand smelt.



The latter is one of the few examples of an immigrating species establishing in a relatively high trophic position. Most of the alien species in the Wadden Sea are suspension feeders in a lower trophic position (Byrnes et al. 2007). These changes on the base of the food web could entail changes to the whole trophic structure. In the example of the sea walnut we assume that the invasive species will not outcompete the native species, even when diets were similar. Nevertheless, grazing pressure on zooplankton is likely to increase. Therefore, occurrence, abundance and position of alien species in the food web of the Wadden Sea is important information for coastal management decisions as detrimental effects of pollution or exploitation on native species could be beneficial to invasive species by releasing them from competition.

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**Eidesstattliche Erklärung**

Hiermit erkläre ich, dass die Abhandlung: "The trophic structure of a Wadden Sea fish community and its feeding interactions with alien species" , abgesehen von der Beratung meines Betreuers Dr. habil. Harald Asmus, nach Inhalt und Form meine eigene Arbeit ist. Sie hat noch nicht im Rahmen eines anderen Prüfungsverfahrens vorgelegen. Ein Kapitel der Arbeit ist in einer wissenschaftlichen Zeitschrift veröffentlicht und zwei Kapitel sind zur Veröffentlichung bei einer wissenschaftlichen Zeitschrift eingereicht worden. Die Arbeit ist unter Einhaltung der Regeln guter wissenschaftlicher Praxis der deutschen Forschungsgesellschaft verfasst worden.

Florian Kellnreitner

# Curriculum Vitae Florian Kellnreitner

## Persönliche Daten

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Geboren am 01.10.1979 in Wien, Österreich  
Diplom Biologe

## Beruflicher Werdegang, Praktika und Weiterbildung

---

Mai 2008-Mai 2011	Anstellung am AWI zur Erstellung der Doktorarbeit an der Wattenmeerstation Sylt (Thema: Das Nahrungsnetz der Fische des Wattenmeeres und Interaktionen mit gebietsfremden Arten)
April 2008	Mitarbeiter beim SPICE II in Indonesien für das AWI; erstellen von UW-Videotransekten zur Fischhäufigkeitsbestimmung im Seegras und Riff.
November 2007-März 2008	Anstellung am AWI: Fischsurvey; Unterwasservideoaufnahmen für Fachgutachten für die Sandentnahmestellen vor Sylt
Juli 2006-September 2007	Hilfswissenschaftlicher Mitarbeiter am AWI
April-September 2005	Praktikum bei AQUASTREAM (Aquakulturbetrieb), Lorient, Frankreich: Optimierung der Produktion der Goldbrasse ( <i>Sparus aurata</i> )
September 2004-September 2005	Studienaustauschprogramm ERASMUS an der ENSAR in Rennes, Frankreich. Spezialisierung: Halieutique (Fischereiwissenschaft)

## Ausbildung

---

Oktober 2007	Diplomprüfung mit Auszeichnung bestanden
Juli 2006-September 2007	Diplomarbeit an der Wattenmeerstation (Sylt) des Alfred Wegener Instituts für Polar- und Meeresforschung (AWI): Populationsdynamik und Produktivität der Strandgrundel <i>Pomatoschistus microps</i> und der Sandgrundel <i>Pomatoschistus minutus</i> (Teleostei: Gobiidae) der Sylt-Rømø Bucht (Deutschland)
September 2002-Juni 2006	Spezialisierung Zoologie an der Universität Wien
Oktober 1999-September 2002	Biologiestudium an der Universität Wien
1990-1998	Gymnasium, GRG 21 Ödenburgerstrasse 74

## Sprachkenntnisse

---

Deutsch (Muttersprache)  
Französisch (Muttersprache)  
Englisch (fließend in Wort und Schrift)  
Spanisch (Grundkenntnisse)

## Weitere Kenntnisse und Erfahrungen

---

Führerschein B	ausgezeichnete Kenntnisse in Microsoft
Deutscher Sportbootführerschein	Word, Excel und Power Point
Deutsches Rettungsschwimmabzeichen Silber	gute Kenntnisse in SigmaPlot, Primer9
Tauchbrevet OWD (PADI)	

## Publikationen

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- Kellnreitner F., Pockberger M., Asmus H., 2011. Seasonal variation of assemblage and feeding guild structure of fish species in a boreal tidal basin. *Estuarine, Coastal and Shelf Science*. doi:10.1016/j.ecss.2011.02.020
- Wegner M., Shama L. N. S., Kellnreitner F., Pockberger M., 2011. Diversity of immune genes and associated gill microbes of European plaice *Pleuronectes platessa*. *Estuarine, Coastal and Shelf Science*. doi:10.1016/j.ecss.2011.09.001
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- Kellnreitner F., Pockberger M., Asmus H., Polte P. Resource partitioning between juvenile herring (*Clupea harengus*) and sand-smelt (*Atherina presbyter*) in the Wadden Sea, North Sea? Submitted to *Estuarine and Coastal Shelf Science*.
- Pockberger M., Kellnreitner F., Asmus R., Asmus H. How significant are small sized fish species for the energy transport in intertidal food webs? Submitted to *Marine Ecology Progress Series*.