



Only a few key prey species fuel a temperate coastal fish food web

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ABSTRACT: The food web structure of a coastal fish community (western Dutch Wadden Sea) was studied based on stomach content data from samples collected between 2010 and 2018. In total, 54 fish species were caught and 72 different prey items were identified. Fish species consumed from only a few up to >30 different prey species, suggesting the presence of both opportunistic and more specialized feeders. We found no significant differences between years or switches in food source with fish size. The trophic positions of the Wadden Sea fish community ranged from 2.0 to 4.7, with most trophic positions above 3.0. In the past, (near)-resident species were the most abundant guild in spring, and juvenile marine migrants in autumn. At present, all guilds are present in similar but low abundances. The (near)-resident community consisted of about 20 species that fed primarily on amphipod crustaceans, brown shrimps and juvenile herring. There was only a slight overlap in diet with the group of juvenile marine migrants (5 species of juvenile flatfishes and clupeids), whose preferred prey were copepods, polychaetes and brown shrimps. About 15 species of marine seasonal visitors showed an overlap in diet with both the (near)-resident and the juvenile marine migrants, especially for brown shrimps and to a lesser extent herring and gobies. Our results illustrate (1) the pivotal position of a few key prey species (amphipod crustaceans, brown shrimps, juvenile herring and gobies) for the coastal Wadden Sea fishes and (2) that the substantial prey overlap in the diet of some predators cannot exclude intra- and inter-specific competition among these predators.

KEY WORDS: Food web structure · Wadden Sea · Stomach content analysis · Fish community · Trophic position · Predator–prey interactions

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1. INTRODUCTION

Temperate coastal zones are dynamic areas, experiencing fluctuations in temperature and salinity on short (tidal) to medium (seasonal) time scales. Since only few species can cope with these rapidly changing conditions, especially temperature and salinity, species diversity in these transition zones between the marine offshore and the freshwater inner zone is relatively low (Levin et al. 2001). Temperate coastal zones are also highly productive ecosystems because of their inputs of nutrients and organic matter from

river runoff and the neighbouring open sea (Nixon 1995, Cloern et al. 2014). Consequently, those species present can occur in high numbers (for example, for the European coast see Gibson 1994, Freitas et al. 2007, 2010, Jung et al. 2017) and thereby attract large numbers of predators. As such, coastal zones are important foraging areas/grounds for a variety of fish, bird and marine mammal species (e.g. Goodall 1983).

One such coastal area is the temperate Wadden Sea, an estuarine area bordering the Dutch, German and Danish North Sea coasts, an important nursery area for a variety of fish species (Zijlstra 1972) and

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also a resting and feeding area for wading birds (Wolff 1983). Over the last decades, the trophic structure of the coastal zone fish fauna has changed and the nursery function of the Wadden Sea for juvenile flatfish has decreased (Tulp et al. 2008, 2017, van der Veer et al. 2011, 2015). A detailed analysis of the present functioning of the Wadden Sea for the various fish species would require detailed information about the different predator–prey relationships. Although some information is available (see for instance Kühl 1961, 1973, de Vlas 1979, Kühl & Kuipers 1983, del Norte-Campos & Temming 1994, Nijssen 2001, Kellnreitner et al. 2012), a comprehensive, detailed analysis of the trophic structure of the coastal Dutch Wadden Sea fish community is still lacking.

Taxonomic identification of prey items using stomach content analysis has been (Hynes 1950) and is still an important tool for the analysis of predator–prey interactions, but it only offers a small temporal snapshot of recently consumed prey items. Nevertheless, all historical data are based on stomach content identification; therefore, any comparison with previous work requires the same methodology. For these reasons, stomach content analysis is still a tool to provide an overview of the most important food web components and predator–prey relationships.

This study elaborates on previous stomach content studies of Wadden Sea fish and analyses the complete fish community of the western Dutch Wadden Sea collected in 2010–2018 with a focus on the competitive interactions between the most important guilds. In addition to (near)-resident species, which are present year-round and spend (almost) their entire life cycle in the area, the study also encompasses juvenile marine migrants using the area as a nursery and marine seasonal (summer or winter) visitors or species visiting the area as adults. Furthermore, marine adventitious visitors, which appear irregularly, diadromous (catadromous or anadromous) migrant species and freshwater adventitious species, which occasionally enter brackish waters, are also found (Zijlstra 1983, Elliott & Dewailly 1995).

In this study, the role and impact of (near)-resident fish species is compared with that of juvenile marine migrants and marine seasonal visitors. Firstly, the trophic structure of the fish community is described based on stomach content information in relation to fish size (or age) following FishBase (Froese & Pauly 2019). Subsequently, the food web structure (trophic position, predator–prey relationships, prey overlap) of the (near)-resident species is determined. Next,

the food web structure for the juvenile marine migrants and marine seasonal visitors is constructed and the extent of overlap and interaction with that of the (near)-resident species is analysed.

Our analysis is based on a long-term monitoring programme of the fish fauna in the western part of the Dutch Wadden Sea by means of fyke nets. The programme started in 1960 and has continued without methodological change until now (van der Veer et al. 2015). Previous papers dealt with long-term patterns in fish abundance and phenology (Cardoso et al. 2015, van der Veer et al. 2015, van Walraven et al. 2017). This study focusses on present food web structure.

2. MATERIALS AND METHODS

2.1. Field sampling

Fish were collected from the catches of a long-term monitoring programme by means of a passive fish trap near the entrance of the Wadden Sea (Fig. 1). This 'kom-fyke' with a stretched mesh size of 20 mm, consisted of a leader of 200 m running from the beach towards deeper waters. Fish swimming against the leader are guided towards 2 chambers (the so-called 'kom') and from there are collected into the fyke. The kom-fyke was emptied every day, weather permitting. During the winter (November–March) and summer (July–August) months, the kom-fyke was removed due to the risk of potential damage by storm and ice in winter and extreme algal blooms and high numbers of jellyfish during summer. For more information, see van der Veer et al. (2015).

All fish caught were taken to the laboratory and sorted within 1 h, identified up to species level, counted and measured for length. During 2010 to 2018, a maximum of 3 individuals per species per week were selected and stored at -20°C for further stomach content analysis.

2.2. Fish abundance

All daily fyke catches for the period 1980–2018 were included for the months April–June and September–October, except those with a fishing duration <12 h (exclusion of 0.1 % of the records), or >48 h (6.6 % of the records), or when the gear was damaged or seriously clogged with debris (0.3 % of the records).

For each catch, numbers per species were determined. Next, weekly and monthly average numbers

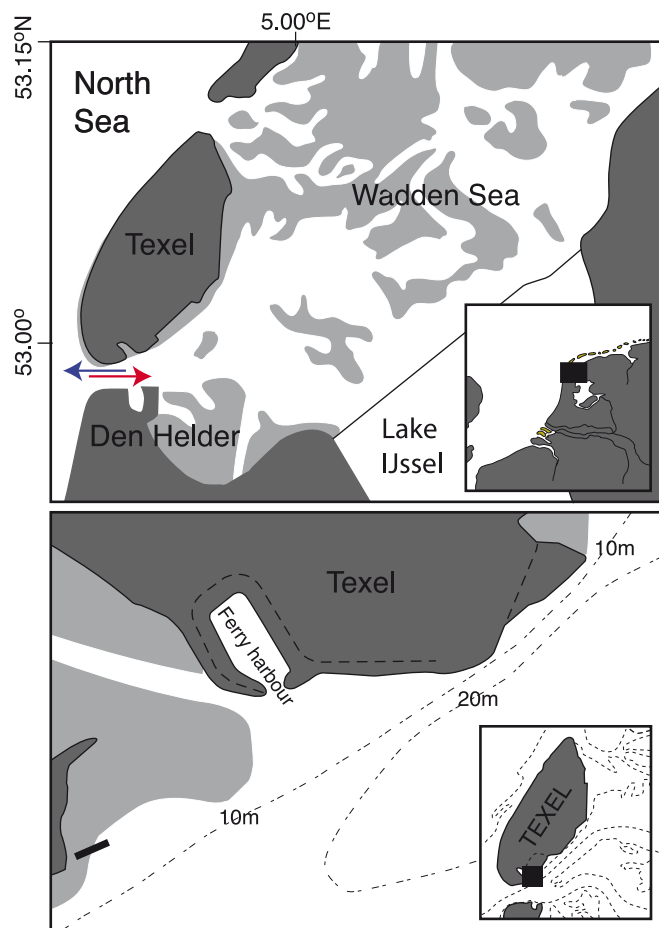


Fig. 1. Sampling location near the island of Texel. Top: western Dutch Wadden Sea (black box); red (blue) arrow indicates inward (outward) migration in spring (autumn). Bottom: fyke net position (black bar). Grey: intertidal areas

caught per fishing day were determined. Finally, mean average catches in spring (April–June) and autumn (September–October) were estimated.

2.3. Stomach content analysis

Within a few weeks of capture, fish selected for dissection were thawed, and total length, fork length, standard length, frozen weight, gonad weight, sex and ripeness were determined. In addition, the sagittal otoliths were removed for age determination. Stomach content was analysed in a petri dish under a dissecting microscope (20×). For each individual fish, the stomach content was weighed (wet mass; g) and the prey items were identified up to species level or if not possible, up to a higher classification (class, order, genus). If possible, total length of the prey was measured (mm). Incomplete specimens, often from species that were eaten in pieces, such

as annelid worms (e.g. *Alitta virens*) or jackknife clams *Ensis leei*, were counted. For each prey item, the percentage of occurrence was calculated (= number of stomachs containing a prey species divided by total number of stomachs examined) as a measure of diet composition following Baker et al. (2014). Taxonomic identification was based on an internal reference collection and Hayward & Ryland (2017) for polychaetes, bivalves and crabs, and on Wheeler (1978) for fish species.

2.4. Data analysis

Functional groups were assigned to all predatory fish species in relation to their use of the Wadden Sea, in line with previous work (van der Veer et al. 2015). These were as follows: pelagic (occurring mainly in the water column, not feeding on benthic organisms); benthopelagic (living and/or feeding on or near the bottom, as well as in midwater) and benthic (living and/or feeding on the bottom), see also FishBase (Froese & Pauly 2019). Each species was classified according to its use of the Wadden Sea area ([near]-resident species, juvenile marine migrants, marine seasonal visitors) based on Witte & Zijlstra (1983), also in line with van der Veer et al. (2015). European bass *Dicentrarchus labrax* was considered to have become a resident species in the Wadden Sea in recent time, due to the presence of small juveniles and adults almost year-round (Cardoso et al. 2015).

For each individual fish and therefore each unique stomach j , the trophic position (TP_j) was not taken directly from FishBase, but was calculated from their diet compositions based on the fixed TP s of prey items and the procedure from FishBase (Froese & Pauly 2019) with a slight modification to compensate for digestion, including the following steps:

Step 1: If all food items were plants or detritus ($TP = 1$), then TP of the predator $TP_j = 1 + 1 = 2$ and standard error (SE) = 0;

Step 2: When there was only 1 food item in the stomach, which was neither a plant nor detritus, then $TP_j = 1 +$ the TP of food item according to FishBase and $SE = SE$ of the food according to FishBase;

Step 3: If there were several food items, at least one of which was not a plant or detritus, then TP was determined based on the relative contributions of each prey to the total diet. To eliminate the effect of the state of digestion on the calculation, the relative contributions of the various prey items to the total diet were determined on the basis of back-calculated

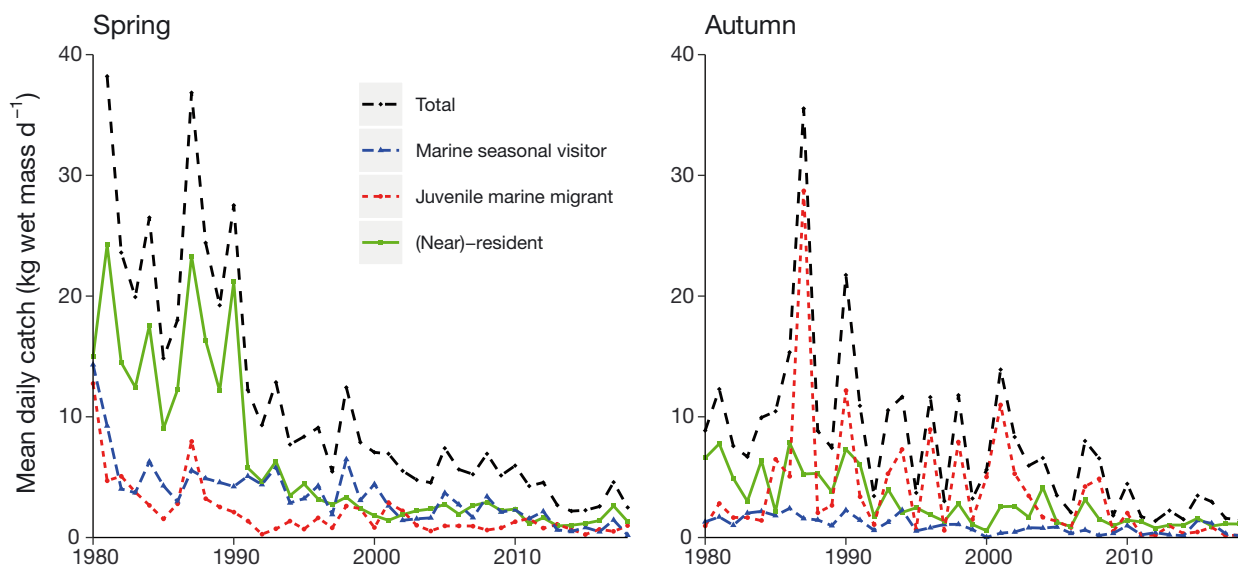


Fig. 2. Mean daily fyke catch (kg wet mass d⁻¹; total and for different guilds individually) in spring and autumn

consumed fresh biomass, reconstructed by means of length–weight relationships. When no length measurement was available (often small prey items), a mean wet mass was taken. The weighted average of the TPs of the various food items was considered to represent the TP of the prey. The TP of the predator was then estimated as $TP_j = 1 + \text{mean weighted TP of all food items inside the stomach}$.

For all species with at least 2 stomach content analyses, mean TP was calculated, and for all species with at least 10 stomach content analyses, prey occurrence was estimated.

All computations and analyses were done in R (R Core Team 2019). The graphics were made using the 'ggplot' package (Wickham 2009).

3. RESULTS

3.1. Fish abundance

Mean fish abundance of the different guilds is shown in Fig. 2. All 3 guilds showed a decrease over time both in spring and in autumn. The decrease was clearer in spring and for the (near)-residents and the juvenile marine migrants. In the 1980s, (near)-resident species were the most abundant guild in spring. From the mid-1990s onwards, abundances of the 3 guilds were low and more or less similar. In autumn, juvenile marine migrants were the most dominant group until about 2010. Thereafter, all guilds were present in similar, but low, numbers.

3.2. Fish community

Over the period 2010–2018, 54 different fish species were caught, and 74 different prey items were identified (Table A1 in the Appendix). Mean TP could be calculated for 51 species and prey composition and occurrence for 41 species.

Number of prey species found in the stomachs showed an increase with the number of stomachs analysed, at least for up to 50 stomachs. Thereafter, the pattern was more variable (Fig. 3). All fishes preyed on multiple species, mostly varying between 3 and 10, up to >30 species, indicating that most fishes were opportunistic feeders.

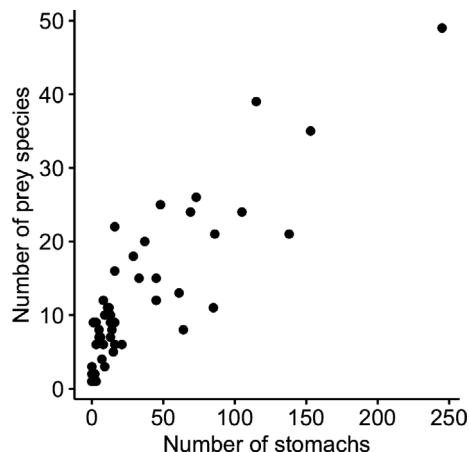


Fig. 3. Number of stomachs analysed for each fish species in relation to the total number of different prey species found inside those stomachs for all study years combined (2010–2018)

For most species, the number of observations and/or size range was too low to analyse any relationship of TP with fish size (Fig. 4). In some species, a slight positive (bass, herring *Clupea harengus*, brill *Scophthalmus rhombus*) or negative (garfish *Belone belone*, lemon sole *Microstomus kitt*, thin-lipped grey mullet *Chelon ramada*) trend between TP and fish size could be observed; however, these relationships were not statistically significant (linear regressions: $p > 0.05$).

The mean TP of the fish community ranged between 2.0 and 4.7, with most TPs above 3.0 (Fig. 5). Low values (< 3.0) were found for the mullet species (*C. ramada*, golden grey mullet *C. aurata* and thick-lipped grey mullet *C. labrosus*). The TP of scad *Trachurus trachurus*, mackerel *Scomber scombrus*, *B. belone*, *S. rhombus*, sea trout *Salmo trutta* and greater sandeel *Hyperoplus lanceolatus* were above 4.0. The marine seasonal visitors showed the largest range of TPs, and the juvenile marine migrants the smallest (Fig. 5).

We found no 1:1 relationship between the mean TP of the fish species in FishBase and the calculated TP based on stomach contents (Fig. 6).

3.3. Differences between guilds

(Near)-resident species varied in TP from 3.2 to 4.7. Their food ranged from copepods to fish species, with a dominance of prey species with a higher TP (Fig. 7). Whereas the diet of some species consisted of a variety of prey items, for a number of species, (multiple) preferred prey items—defined as items with an occurrence in the stomachs of $> 25\%$ —could be identified and a number of prey items occurred in the stomachs with a presence of 50% or more. Stickleback *Gasterosteus aculeatus* preferred copepods; viviparous blenny *Zoarces viviparus*: copepods and sand hoppers; butterfish *Pholis gunnellus*: sand hoppers; hooknose *Agonus cataphractus* and sea snail *Liparis liparis*: shrimps ($> 50\%$); bass *Dicentrarchus labrax*: shrimps and herring *Clupea harengus*; sea scorpion *Taurulus bubalis*: shore crabs ($> 50\%$) and shrimps; bull-rout *Myoxocephalus scorpius*: shrimps ($> 50\%$); flounder *Platichthys flesus*: shrimps; greater pipefish *Syngnathus acus*: shrimps ($> 50\%$); five bearded rockling *Ciliata mustela*: shrimps ($> 50\%$); Gobiidae (gobies): shrimps and fish ($> 50\%$); twaite shad *Alosa fallax*: shrimps and herring; garfish *Belone belone*: herring ($> 50\%$) and fish; and sea trout *Salmo trutta*: herring and sandeel ($> 50\%$).

There was a large overlap in prey species consumed by the various (near)-resident species, with a few prey items having a high occurrence (sand hoppers, brown shrimps and juvenile herring) in the stomachs of different fish species; however, for a large number of prey items their occurrence in the stomachs was low (Fig. 7).

Juvenile marine migrants consisted mainly of flat-fish species and clupeids that had a TP between 3.2 and 3.4 (Fig. 7). Juvenile marine migrants also preyed upon a variety of prey items, most of them in low occurrence in the stomachs. Herring *Clupea harengus* were cannibalistic. For herring and sprat *Sprattus sprattus*, copepods were a preferred prey, for plaice *Pleuronectes platessa* and sole *Solea solea* it was polychaetes. All species consumed brown shrimps. For these three prey species, overlap in diet occurred between marine juvenile migrants. With (near)-resident species, overlap in diet occurred for copepods, sand hoppers, brown shrimps and herring.

Marine seasonal visitors consisted of a variety of species with a TP between 2.4 and 4.7 (Fig. 7). Most marine seasonal visitors also preyed on multiple prey items, mostly with a low frequency of occurrence. For most marine seasonal visitors, brown shrimps and herring were preferred prey items. Furthermore, sandeel *Ammodytes tobianus* preferred Mysidae; dab *Limanda limanda*: Atlantic jackknife clam and shore crabs; lesser weever *Echiichthys vipera*: Atlantic jackknife clam; scaldfish *Arnoglossus laterna*: Mysidae; turbot *Scophthalmus maximus*: sand goby; brill *Scophthalmus rhombus*: sand- and common goby; and greater sandeel *Hyperoplus lanceolatus* preferred fishes. Overlap in diet with (near-) resident and marine juvenile migrant species occurred mainly for brown shrimps and to a lesser extent for herring and fish.

A principal component analysis (PCA) was used to visualize the differences and similarities between the various fish species with respect to their main prey items. The relation between the predatory fish species and prey was based on the average prey biomass found inside the stomachs of the predators in all years combined. The PCA illustrated the clustering around algae, copepods, Atlantic jackknife clam, brown shrimps, shore crab and herring as main prey items (Fig. 8).

4. DISCUSSION

Food web analysis requires a spatial and temporal sampling of the important food at the appropriate spatial and temporal scales. Ideally, it would combine different sampling gears in various habitats and loca-

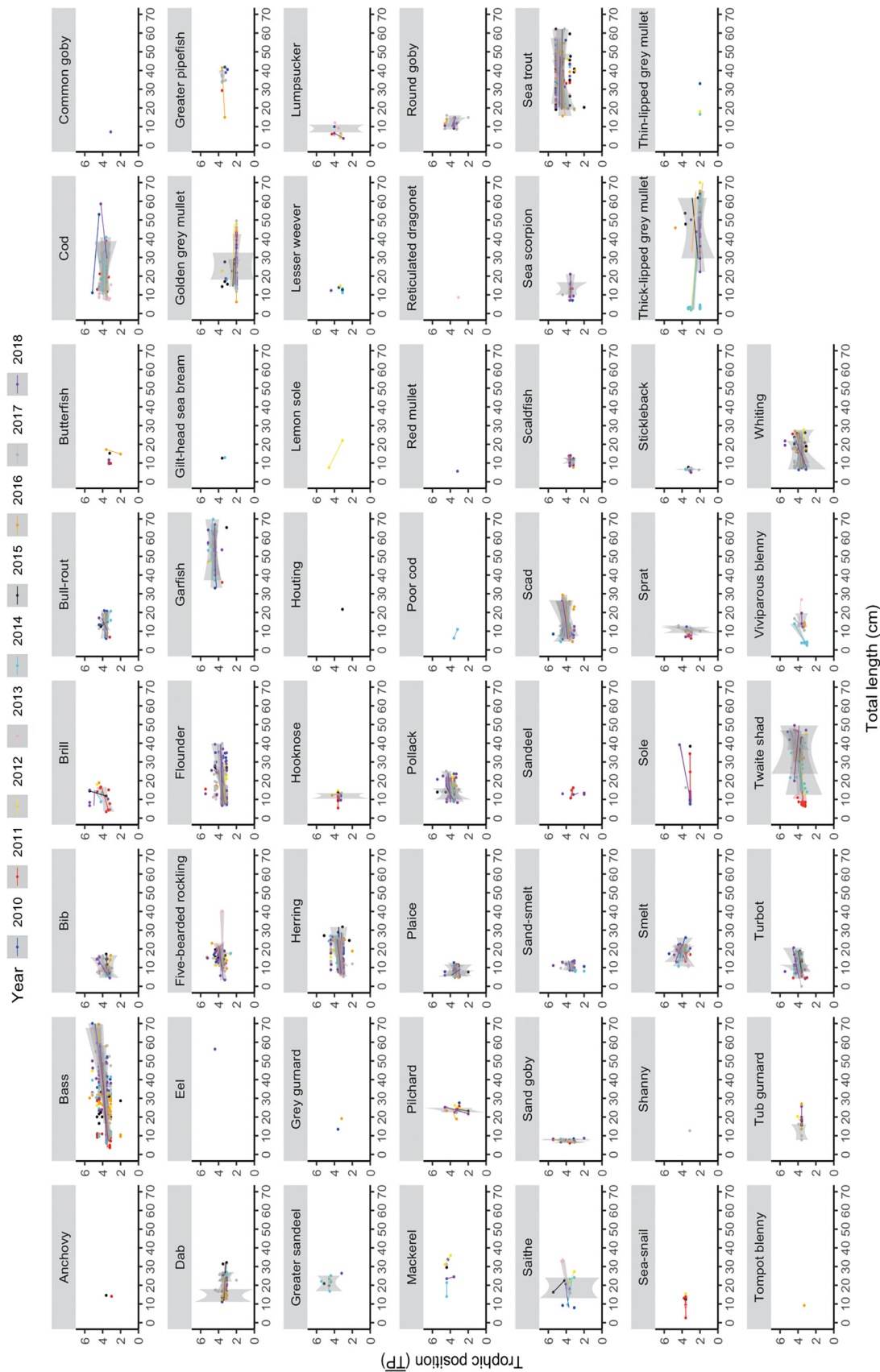
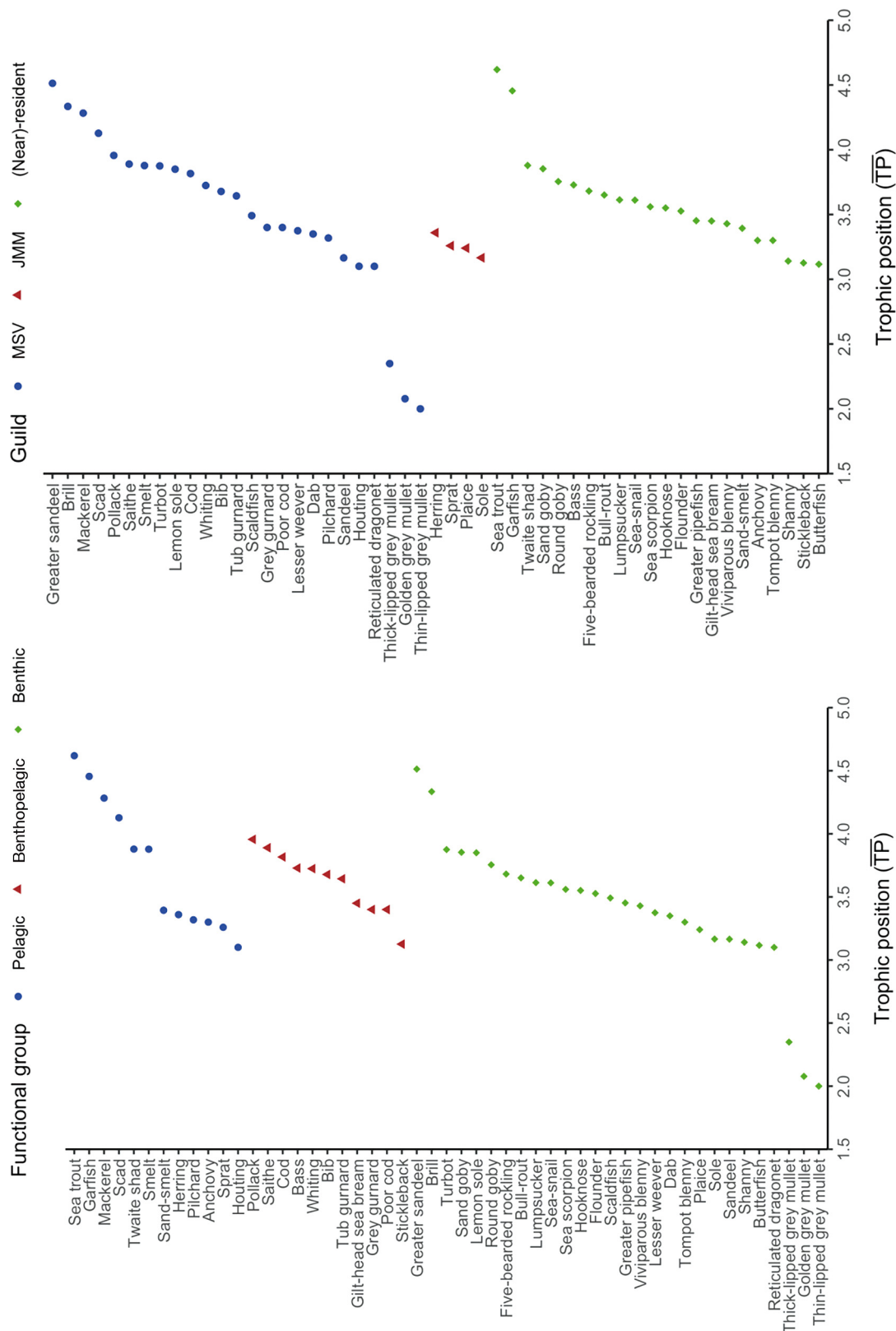


Fig. 4. Calculated mean trophic positions based on the stomach content as a function of the total length for each predatory species. A linear regression with a 95 % confidence interval for each year (2010–2018) is added to visualize trends



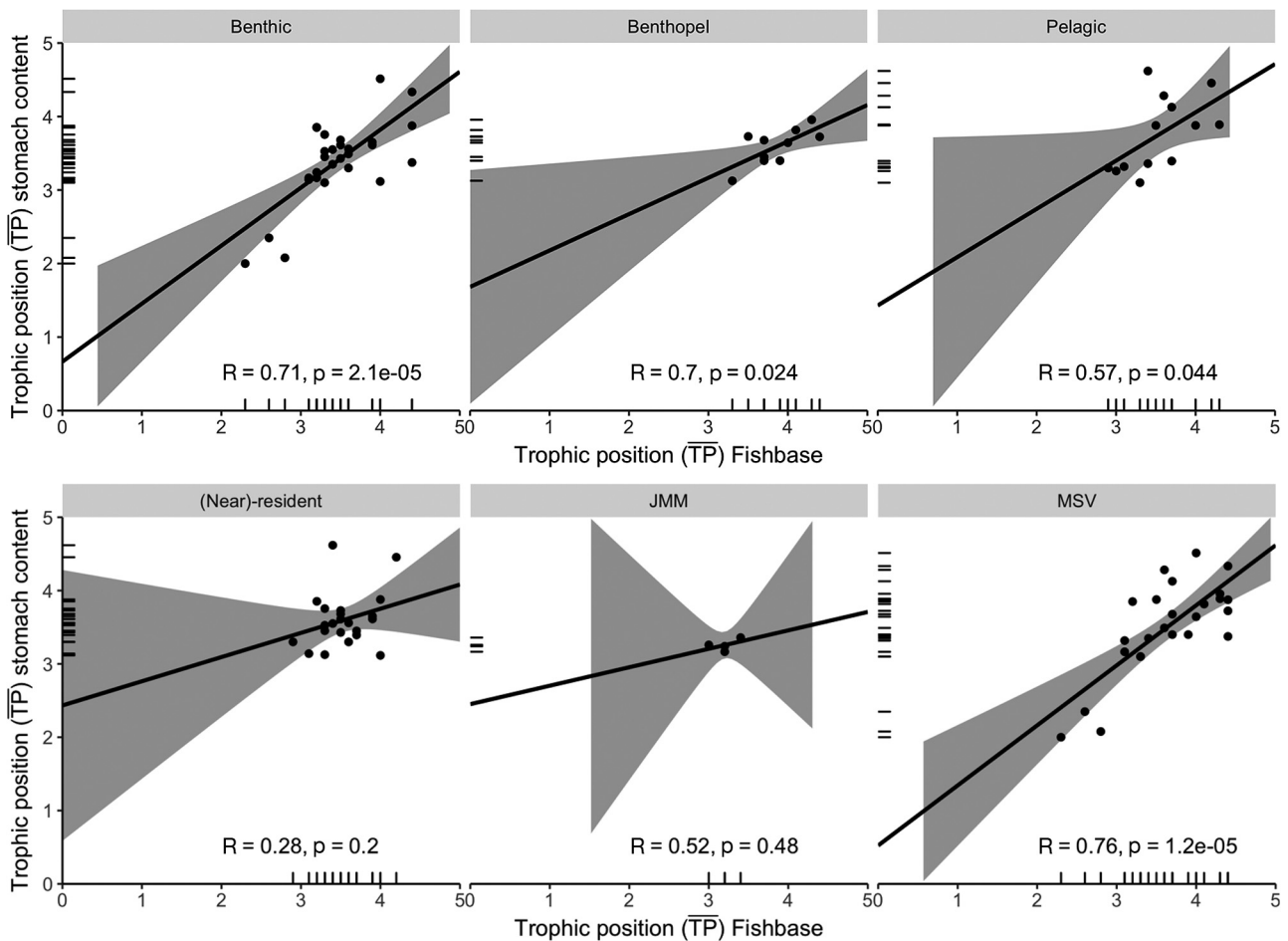


Fig. 6. Linear relationship with 95% confidence interval between mean trophic position (TP) from FishBase and the mean TP based on the stomach content analysis. Top: functional group; bottom: guilds (JMM: juvenile marine migrant; MSV: marine seasonal visitor)

tions over a number of years. The sampling design in this study is limited to a single gear at a single spot. Nevertheless, the large number of species caught by the kom-fyke ($n = 54$) is comparable to Kellnreitner et al. (2012) in the Sylt-Rømø bight, Germany ($n = 43$). Over the time period 1960–2015, 82 fish species were caught by the kom-fyke (van der Veer et al. 2015), indicating that in our study, some species were likely missed and others were caught in low numbers.

Sampling was performed during the period of fish immigration in spring and emigration in autumn only. Although no differences between spring and autumn were found, this pattern may not hold true for the summer and winter period, as was found by Kellnreitner et al. (2012) in the German Wadden Sea. The large number of (near)-resident, juvenile marine migrants and marine seasonal visitors caught belong to different functional groups (benthic, benthopelagic, pelagic), indicating that they represent different habitats. Furthermore, the predator–prey relationships found in

this study corresponded with the general food relationships found for Wadden Sea fishes in the past as summarized by Kühl & Kuipers (1983) and recently in the Sylt-Rømø bight, Germany, by Kellnreitner et al. (2012), suggesting that our results might be applicable to an area larger than the western Dutch Wadden Sea.

All species analysed consumed a variety of prey items. However, taxonomic identification of prey items via stomach content analysis only offers a small snapshot in time, as it details only recently ingested prey items, and regurgitation and digestion are factors that result in missed or overlooked prey items. While our extended period of sampling may have partly overcome these limitations, the relationship between the number of stomachs analysed and the number of prey species found in the stomachs does not seem to level off above 50 stomachs, indicating that for the rare species or for species having a very wide diet, insufficient stomachs may have been sampled to cover all possible prey species (Mulas et al. 2015).

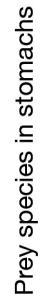


Fig. 7. Occurrence of prey species (%) in the stomach of fish species in the years 2010–2018 together with corresponding calculated trophic position (TP) and guild. Predatory fish species are listed by guild type from lowest to highest TP, and prey species are listed from lowest to highest TP

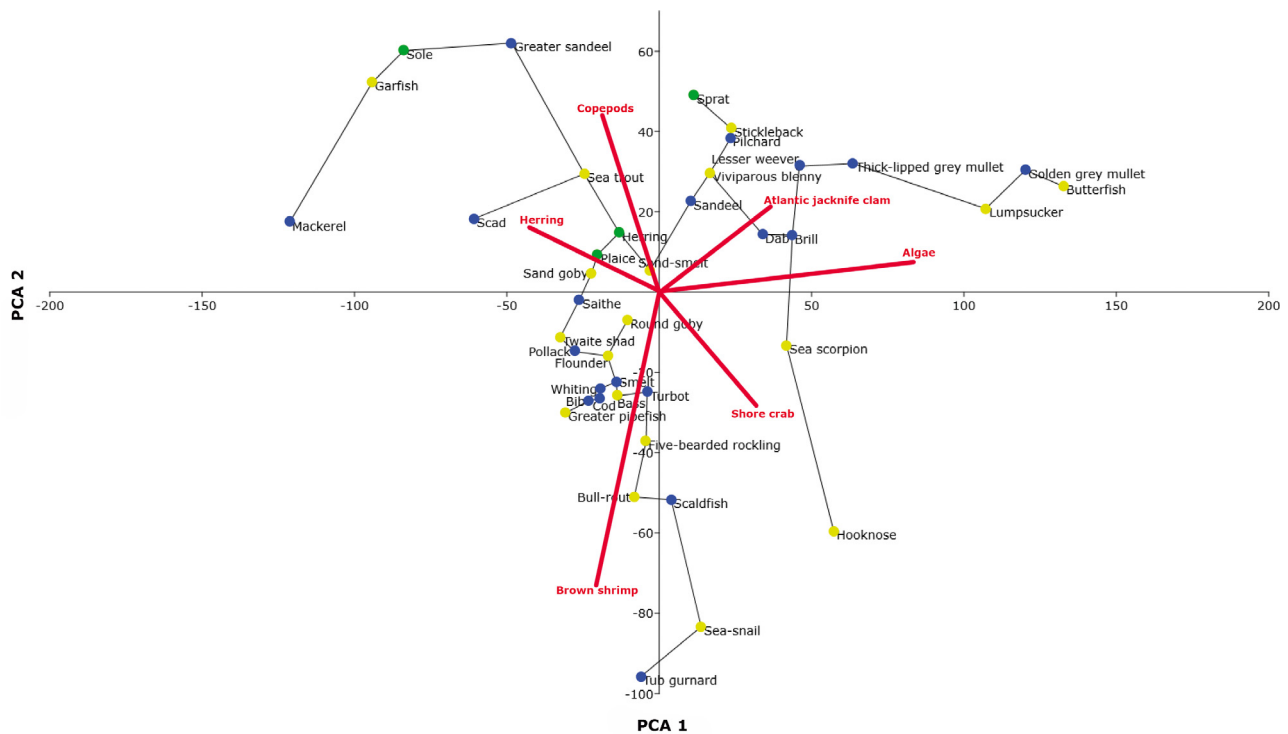


Fig. 8. PCA per species for each guild based on stomach contents. Yellow dots: (near)-residents, blue dots: marine seasonal visitors, green dots: juvenile marine migrants. The PCA illustrates the clustering around algae, copepods, brown shrimps and herring (shown in red)

4.1. Trophic structure

This study shows that the trophic information provided by FishBase allows an impression of the trophic structure of a fish community: information from FishBase correlates significantly with estimates based on stomach content composition. However, for the Dutch Wadden Sea, except for the marine seasonal visitors, the information from FishBase gave an underestimation of the TPs calculated from the stomach contents. This might be caused by differences in size or age between this study and the reference values of FishBase, given the positive relationship between fish size and TP (see for instance Ursin 1973). These relationships have also been observed in other studies, e.g. with growing juvenile cod and plaice (Daan 1973, Kuipers 1977). No significant relationships between fish size and TP were found in this study, but the sizes and ages of the (near)-resident species and juvenile marine migrants were relatively small, and only marine seasonal visitors included larger fish and more adults (van der Veer et al. 2015, van Walraven et al. 2017). Another factor might be area-specific differences in feeding patterns or the contributions of different items to the diet for both (near)-resident species and juvenile marine migrants. For instance, the

sand goby *Pomatoschistus minutus*, a (near)-resident species, mainly consumes the amphipod *Corophium volutator* in Swedish bays (Pihl 1985) and small shrimp *Crangon crangon* in the Dutch Wadden Sea (Kühl & Kuipers 1983). Differences also occurred for juvenile marine migrants. For 0-group plaice, an important contribution of *Corophium volutator* to the diet was found in Swedish bays (Pihl 1985), while at the Balgzand intertidal in the Dutch Wadden Sea, tail-tips and bivalve siphons were the most important components of the diet (de Vlas 1979).

In terms of species and abundance, the main components of the coastal Wadden Sea fish fauna were (near)-resident species, juvenile marine migrants and marine seasonal visitors. The TP of the (near)-resident species ranged from 3.2 to 4.7, meaning that these (near)-resident species include more secondary consumers (carnivores) and tertiary consumers (carnivores consuming other carnivores). The juvenile marine migrants covered a narrow range in TP from 3.2 to 3.4, reflecting that these juveniles are not tertiary consumers. Marine seasonal visitors had the largest range, 2.4 to 4.7, and included herbivores up to tertiary consumers.

The TPs of the present fish community illustrate that the trophic structure still covers the various levels up to tertiary consumers, despite the disappear-

ance of species such as some skates and sharks (Wolff 2000, Lotze 2007). The observed degradation of trophic structure and nursery function over the last decades (van der Veer et al. 2015) might not be a result of loss of TPs, but rather a result of strong reductions in abundance of various TPs due to a large decrease in abundance (Tulp et al. 2008, van der Veer et al. 2015). The importance of the Wadden Sea as a nursery area (Zijlstra 1972) is still observed and reflected in the increased catches of juvenile marine migrants in autumn compared to spring.

4.2. Food web structure

Stomach content analysis showed that all species consumed multiple prey items, suggesting opportunistic feeding. On the other hand, for most species preferred prey items could be identified, suggesting at least some kind of specialization. Cluster analysis of the stomach contents supports this, with clustering evident around algae, copepods, polychaetes, brown shrimps and herring. This clustering was also partly found in the German Wadden Sea (Kellnreitner et al. 2012) and corresponds with the classification of Wadden Sea fish by Kühl & Kuipers (1983) into those feeding on (1) minute particles from the bottom, (2) zooplankton, (3) zoobenthos and (4) fish.

Notably, (near)-resident species and marine seasonal visitors showed dietary overlap in prey items, indicating that for some predators, intra- and inter-specific competition cannot be excluded. The decrease in fish abundance over the last decades (Tulp et al. 2008, van der Veer et al. 2015, this study) suggests that competition will be less likely now than in the past.

Juvenile marine migrants appear to have their own niche: the clupeids prey mainly on copepods while juvenile flatfishes prefer polychaetes. In terms of energy, the nursery function of the area is mainly to convert energy: the energy influx of the massive amounts of marine migrant larvae is on the same order of magnitude as the energy export of larger juveniles at the end of the growing season (Wolff 1980).

In the Dutch Wadden Sea, juvenile herring and brown shrimps are abundant and are the most preferred prey items of many fish species, and thereby form important links in the fish food web. Juvenile herring form a link from plankton to secondary consumers by their consumption of copepods (Last 1989), while brown shrimps (Wolff & Zijlstra 1983, Pihl & Rosenberg 1984) link the benthos to secondary consumers by their consumption of (epi)benthic prey items. Copepods, brown shrimps and mysid shrimps

were also the most abundant prey items of fish in the Sylt-Rømø bight, Germany (Kellnreitner et al. 2012), indicating that at a large geographic scale, key prey items for the fish community are the same, although their contribution might vary due to differences in absolute and relative prey and predator abundance.

4.3. Top-down or bottom-up control

Similar to other estuarine food webs, the Wadden Sea food web is supported by local pelagic and benthic primary production, as well as the import of dead organic matter from the open sea and freshwater discharges (see de Jonge & Postma 1974, Kuipers et al. 1981, de Wilde & Beukema 1984, de Jonge 1990). In the Dutch part, benthic primary producers (microphytobenthos) are the most important energy source for the majority of consumers in the food web, but in line with Deegan & Garritt (1997), large spatial heterogeneity was observed (Christianen et al. 2017). Recently, Jung et al. (2019) highlighted the important role of the influx of freshwater carbon as an energy source, indicating that the importance of the various energy sources might vary spatially as well as temporally.

There has long been discussion as to whether trophic control in these continental shelf ecosystems is bottom-up (resource-driven) or also top-down (consumer driven). Jones (1989) argued that historically, before exploitation started in general, fish populations might have been determined by resource limitations. Anecdotal information indicates that fish biomass in the Wadden Sea was substantially higher in the past, even allowing a community of fisherman to make a living with passive fyke nets, until this came to an end around the 1960s due to decreasing catches. However, this did not stop a further decrease in fish abundance in the area, especially from the 1980s onwards (Tulp et al. 2008, 2017, van der Veer et al. 2015). It is therefore questionable that at present the trophic control of the fish community in the temperate coastal Wadden Sea would be bottom-up (resource-driven).

Frank et al. (2007) provided evidence that the type of trophic forcing might be strongly correlated with species richness and temperature, whereby very cold and species-poor areas might succumb to top-down control. Although only a few fish species are abundant, species richness in the Wadden Sea is still substantial, with about 100 different species having been recorded (Witte & Zijlstra 1983). On the other hand, however, species abundance has seriously

declined over the last decades (Tulp et al. 2008, 2017, van der Veer et al. 2015). Furthermore, the area is situated in the temperate zone, where temperatures are not notably low. Also, the fact that most Wadden Sea fish species are not highly specialized predators but rather opportunistic feeders makes resource limitation less likely. On the other hand, resource limitation might be an issue since the Wadden Sea fish food web structure relies on only a few abundant species, especially juvenile herring and brown shrimps that are the preferred prey items of most fish species.

Various methods have been suggested to analyse bottom-up control, such as the proportion of prey production that is consumed by their predators (Evans 1984), per capita population growth rate in relation to the population density of a habitat in line with MacCall's theoretical basin model (MacCall 1990) in the form of metabolic biomass (van der Veer et al. 2000), applying self-thinning (Nash et al. 2007), and the analysis of the growth potential (van der Veer & Witte 1993, Freitas et al. 2007). Most studies have been conducted on demersal fish, with partially contradictory results. Recently, Chevillot et al. (2019) concluded, based on an Ecopath modelling exercise, that the Gironde estuary reached its trophic carrying capacity with resource limitation for demersal fish. Also Day et al. (2020) and Saulnier et al. (2020) suggested the occurrence of trophic limitation for juvenile marine migrants based on estimates of benthic production. On the other hand, a detailed seasonal growth analysis for a (near)-resident species in the Wadden Sea, *P. minutus*, indicated that growth was not food-limited (Freitas et al. 2011), suggesting the absence of such a bottom-up control. For some juvenile marine migrants, i.e. juvenile flatfishes, both van der Veer et al. (2000) and Nash et al. (2007) concluded that these populations rarely approached the carrying capacity of the nursery grounds. To what extent this also holds true for pelagic juvenile marine species (herring, sprat) and (near)-residents is unclear. Control may be linked to latitude (temperature) as suggested by Frank et al. (2007), but also to feeding guild, whereby especially zooplankton feeders such as herring (juvenile marine migrants) and fish feeders (such as much of the marine seasonal visitors) are more sensitive to bottom-up control.

A food web that depends on a few abundant species might be a characteristic of temperate coastal areas in general; these are highly productive systems due to nutrient and organic matter inputs (Nixon 1995, Cloern et al. 2014), and only a few species can cope with their rapidly changing abiotic conditions (Levin et al. 2001). This is in line with the observation

by Rice (1995) that in many marine food webs, particularly in boreal and subboreal areas, a single taxon in an intermediate TP transfers most of its energy to higher predators.

Data archive. Original data and R script for calculations can be found under <https://dx.doi.org/10.25850/nioz/7b.b.bb>.

Acknowledgements. Thanks to all of our colleagues who assisted in the collection and analyses of the samples, especially Rob Dapper, Ewout Adriaans, Willem Jongejan, Sieme Gieles and Marco Kortenhoeven. Nelleke Barten-Krijgsman assisted in the final preparation of the figures. All fish sampling and handling was done under CCD project number AVD8020020174165.

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Appendix. Additional information

Table A1. General information of species analysed. TP: trophic position; MSV: marine seasonal visitor; JMM: juvenile marine migrant

| Species | Binomial | TP calculated by stomach content | TP according to FishBase | Functional group | Guild |
|--------------------------|---------------------------------|-------------------------------------|-----------------------------|---------------------|-----------------|
| Anchovy | <i>Engraulis encrasicolus</i> | 3.3 | 2.9 | Pelagic | (Near)-resident |
| Bass | <i>Dicentrarchus labrax</i> | 3.7 | 3.5 | Benthic | (Near)-resident |
| Bib | <i>Trisopterus luscus</i> | 3.7 | 3.7 | Benthopelagic | MSV |
| Brill | <i>Scophthalmus rhombus</i> | 4.3 | 4.4 | Benthic | MSV |
| Bull-rout | <i>Myoxocephalus scorpius</i> | 3.7 | 3.9 | Benthic | (Near)-resident |
| Butterfish | <i>Pholis gunellus</i> | 3.1 | 4 | Benthic | (Near)-resident |
| Cod | <i>Gadus morhua</i> | 3.8 | 4.1 | Benthopelagic | MSV |
| Dab | <i>Limanda limanda</i> | 3.3 | 3.4 | Benthic | MSV |
| Five-bearded rockling | <i>Ciliata mustela</i> | 3.7 | 3.5 | Benthic | (Near)-resident |
| Flounder | <i>Platichthys flesus</i> | 3.5 | 3.3 | Benthic | (Near)-resident |
| Garfish | <i>Belone belone</i> | 4.5 | 4.2 | Pelagic | (Near)-resident |
| Gilt-head sea bream | <i>Spanus aurata</i> | 3.5 | 3.7 | Benthopelagic | (Near)-resident |
| Golden grey mullet | <i>Chelon aurata</i> | 2.1 | 2.8 | Benthic | MSV |
| Greater pipefish | <i>Syngnathus acus</i> | 3.5 | 3.3 | Benthic | (Near)-resident |
| Greater sandeel | <i>Hyperoplus lanceolatus</i> | 4.5 | 4 | Benthic | MSV |
| Grey gurnard | <i>Eutrigla gurnardus</i> | 3.4 | 3.9 | Benthopelagic | MSV |
| Herring | <i>Clupea harengus</i> | 3.4 | 3.4 | Pelagic | JMM |
| Hooknose | <i>Agonus cataphractus</i> | 3.6 | 3.4 | Benthic | (Near)-resident |
| Houting | <i>Coregonus oxyrinchus</i> | 3.1 | 3.3 | Pelagic | MSV |
| Lemon sole | <i>Microstomus kitt</i> | 3.9 | 3.2 | Benthic | MSV |
| Lesser weever | <i>Echeiichthys vipera</i> | 3.4 | 4.4 | Benthic | MSV |
| Lumpsucker | <i>Cyclopterus lumpus</i> | 3.6 | 3.9 | Benthic | (Near)-resident |
| Mackerel | <i>Scomber scombrus</i> | 4.3 | 3.6 | Pelagic | MSV |
| Pilchard | <i>Sardine pilchardus</i> | 3.3 | 3.1 | Pelagic | MSV |
| Plaice | <i>Pleuronectes platessa</i> | 3.2 | 3.2 | Benthic | JMM |
| Pollack | <i>Pollachius pollachius</i> | 4.0 | 4.3 | Benthopelagic | MSV |
| Poor cod | <i>Trisopterus minutus</i> | 3.4 | 3.7 | Benthopelagic | MSV |
| Reticulated dragonet | <i>Callionymus reticulatus</i> | 3.1 | 3.3 | Benthic | MSV |
| Round goby | <i>Neogobius melanostomus</i> | 3.8 | 3.3 | Benthic | (Near)-resident |
| Saithe | <i>Pollachius virens</i> | 3.9 | 4.3 | Pelagic | MSV |
| Sand goby | <i>Pomatoschistus minutus</i> | 3.9 | 3.2 | Benthic | (Near)-resident |
| Sand-smelt | <i>Atherina presbyter</i> | 3.4 | 3.7 | Pelagic | (Near)-resident |
| Sandeel | <i>Ammodytes tobianus</i> | 3.2 | 3.1 | Benthic | MSV |
| Scad | <i>Alosa alosa</i> | 4.1 | 3.7 | Pelagic | MSV |
| Scaldfish | <i>Arnoglossus laterna</i> | 3.5 | 3.6 | Benthic | MSV |
| Sea scorpion | <i>Taurulus bubalis</i> | 3.6 | 3.6 | Benthic | (Near)-resident |
| Sea trout | <i>Salmo trutta</i> | 4.6 | 3.4 | Pelagic | (Near)-resident |
| Sea-snail | <i>Liparis liparis</i> | 3.6 | 3.5 | Benthic | (Near)-resident |
| Shanny | <i>Lipophrys pholis</i> | 3.1 | 3.1 | Benthic | (Near)-resident |
| Smelt | <i>Osmerus eperlanus</i> | 3.9 | 3.5 | Pelagic | MSV |
| Sole | <i>Solea solea</i> | 3.2 | 3.2 | Benthic | JMM |
| Sprat | <i>Sprattus sprattus</i> | 3.3 | 3 | Pelagic | JMM |
| Stickleback | <i>Gasterosteus aculeatus</i> | 3.1 | 3.3 | Benthopelagic | (Near)-resident |
| Thick-lipped grey mullet | <i>Chelon labrosus</i> | 2.3 | 2.6 | Benthic | MSV |
| Thin-lipped grey mullet | <i>Chelon ramada</i> | 2.0 | 2.3 | Benthic | MSV |
| Tompot blenny | <i>Parablennius gattorugine</i> | 3.3 | 3.6 | Benthic | (Near)-resident |
| Tub gurnard | <i>Chelidonichthys lucerna</i> | 3.6 | 4 | Benthopelagic | MSV |
| Turbot | <i>Scophthalmus maxima</i> | 3.9 | 4.4 | Benthic | MSV |
| Twaite shad | <i>Alosa fallax</i> | 3.9 | 4 | Pelagic | (Near)-resident |
| Viviparous blenny | <i>Zoarces viviparus</i> | 3.4 | 3.5 | Benthic | (Near)-resident |
| Whiting | <i>Merlangus merlangus</i> | 3.7 | 4.4 | Benthopelagic | MSV |