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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 from 2010 to 2018. In total 54 fish species were caught and 72 different prey items were identified. Fish species had consumed from a few up to more than 30 different prey species, suggesting the presence of both opportunistic and more specialized feeders. No significant differences between years nor switches in food source with fish size were found. The trophic positions of the Wadden Sea fish community ranged between 2.0 and 4.7, with most trophic positions above 3.0. In the past, (near)-resident species were the most abundant functional group in spring and juvenile marine migrants in autumn. Nowadays, all functional groups are present in almost similar but low abundances. The (near)-resident community consisted of about 20 species which especially were feeding on amphipod crustaceans, brown shrimps and juvenile herring. There was only a slight overlap in diet with the group of marine juvenile migrants (5 species of juvenile flatfishes and clupeids), whose preferred preys

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 marine juvenile migrant 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 for the coastal Wadden Sea fishes: amphipod crustaceans, brown shrimps, juvenile herring and gobies, and that (2) the substantial prey overlap in the diet of some predators cannot exclude some intra- and inter-specific competition for some predators.

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 of 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 [see for the European coast for instance Gibson (1994), Freitas et al. (2007, 2010), Jung et al. (2017)] and thereby also attracting large numbers of predators. As such, coastal zones are important foraging areas/grounds for a variety of fish, bird and marine mammal species [see for instance Goodall (1983)].

One such coastal area is the temperate Wadden Sea, an estuarine area bordering the Dutch, German and Danish North Sea coast, an important nursery area for a variety of fish species (Zijlstra 1972) and 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 flatfish juveniles 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 various predator-prey relationships. Although some information is available (see for instance Kühl 1961, 1973, de Vlas 1979, Kühl & Kuipers 1983, 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, however it only offers a small temporal snapshot of recent prey items only. Nevertheless, all historical data is 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 functional groups. In addition to (near)-resident species, present year-round and spending (almost) their entire live-cycle in the area, the study also encompases marine juvenile migrants using the area as a nursery and marine seasonal (summer of winter) visitors or users visiting the area as adults. Furthermore, marine adventitious visitors, which appearing 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 marine juvenile migrants and marine seasonal (summer of winter) visitors. Firstly, the trophic structure of the fish community will be 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 marine juvenile migrants and marine seasonal visitors is constructed and the extend of overlap and interaction with that of the (near)-resident species 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 (van der Veer et al. 2015, Cardoso 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 200m running from the beach towards deeper waters. Fish swimming against the leader are guided towards two chambers (the so-called 'kom') and from there 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 an hour, identified up to species level, counted and their length measured. During 2010 to 2018, a maximum of three individuals per species per week (Monday – Sunday) 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 less than 12 h (exclusion of 0.1% of the records), or more than 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 (Monday – Sunday) and monthly average numbers caught per fishing day were determined. Finally, mean average catch in spring (April – June) and autumn (September – October) was estimated.

2.3. Stomach content analysis

Within a few weeks of capture, fish selected for dissection were defrosted 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 binocular (20x). For each individual fish, the stomach content was weighted (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). Also, if possible, total length of the prey was measured (mm). Incomplete specimens, often from species that were eaten in pieces such as *Alitta virens* or *Ensis leei*, were counted. For each prey item percentage of occurrence was calculated (= number of stomachs containing a prey species divided by total number of stomachs examined) as 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 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). Furthermore, species were classified according to their use of the Wadden Sea area [(near)-resident species, marine juvenile migrants, marine seasonal visitors] based on Witte & Zijlstra (1983), also in line with van der Veer et al. (2015). *Dicentrarchus labrax* (bass) 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 calculated from their diet compositions based on the fixed trophic positions 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 trophic position of the predator $TP_j = 1 + 1 = 2$ and standard error (s.e.) = 0;

Step 2: In case there was only one food item in the stomach, which was neither a plant nor detritus then: TP_j = 1 + the trophic position TP of food item according to FishBase and s.e. = s.e. of the food according to FishBase;

Step 3: If there were several food items, and at least one was not a plant or detritus, then trophic position 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 contribution of the various prey item to the total diet was determined on the basis of back-calculated 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 trophic positions of the various food items was considered to represent the trophic position of the prey. The trophic position of the predator was estimated according to:

TP_j = 1 + mean weighted trophic position of all food items inside the stomach.

For all species with at least 2 stomach contents analyses, mean trophic position was calculated, and for all species with at least 10 stomach contents 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 functional groups is shown in Fig 2. All three groups showed a decrease in time both in spring and in autumn. The decrease was clearer in spring and for the (near)-resident and the marine juvenile migrants. In the 1980s, (near)-resident species were the most abundant functional group in spring. From the mid 1990s onwards, abundance of the three groups was low and more or less similar. In autumn, marine juvenile migrants were the most dominant group until about 2010. Hereafter, all functional groups 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 (Supplementary information Table S1). Mean trophic position 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 number of stomachs analysed, at least for up to 50 stomachs. Hereafter, the pattern was more variable (Fig 3). All fishes were preying on multiple species, mostly varying between 3 and 10 to up to more than 30 species, indicating that most fishes were opportunistic feeders.

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

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

There was 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 functional groups

(Near)-resident species varied in trophic position 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.

Gasterosteus aculeatus (stickleback) preferred copepods; *Zoarces viviparus* (viviparous blenny): copepods and sand hoppers; *Pholis gunnellus* (butterfish): sand hoppers; *Agonus cataphractus* (hooknose) and *Liparis liparis* (sea snail): shrimps (> 50%); *Dicentrarchus labrax* (bass): shrimps and *Clupea harengus* (herring); sea scorpion: shore crabs (>50%) and shrimps; bull-rout: shrimps (>50%); flounder: shrimps; greater pipefish: shrimps (>50%); five bearded rockling: shrimps (>50%); gobies: shrimps and fish (>50%); twaite shed: shrimps and *Clupea harengus* (herring),; garfish: herring (>50%) and fish and sea trout: *Clupea harengus* (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).

Marine juvenile migrants consisted mainly of flatfish species and clupeids and they had a trophic position between 3.2 and 3.4 (Fig 7). Marine juvenile migrants also preyed upon a variety of prey items, most of them in low occurrence in the stomachs. Herring were cannibalistic. For herring and sprat, copepods were a preferred prey, for plaice and sole 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 trophic position 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 preferred Mysidae; dab: Atlantic jackknife clam and shore crabs; lesser weever: Atlantic jackknife clam; scaldfish: Mysidae; turbot: sand goby; brill: sand- and common goby and greater sandeel 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 the 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 all years combined. The PCA illustrated the clustering around algae, copepods, polychaetes, brown shrimps 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 locations 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 (54) is comparable to

Kellnreitner et al. (2012) in the Sylt-Rømø bight, Germany (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 this study some species will be missed and some others are 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, it cannot be guaranteed that this does not hold true for the summer and winter period as has been found by Kellnreitner et al. (2012) in the German Wadden Sea. The large number of (near)-resident, marine juvenile migrants and marine seasonal visitors caught belong to different functional groups (pelagic, benthopelagic, demersal) 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 the results of this study might be applicable for a larger area than the western Dutch Wadden Sea only.

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, while regurgitation and digestion are factors that result in missing or overlooking prey items. While our extended period of sampling may have partly overcome these limitations, the relationship between number of stomachs analysed and number of prey species found in the stomachs does not seem to level off below 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).

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 trophic positions 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 that there is a positive relationship between fish size and trophic position (see for instance Ursin 1973). These relationships have also been observed in other studies such as growing juvenile cod and plaice (Daan 1973, Kuipers 1977). No significant relationships between fish size and trophic position were found in this study, but the size and age of the (near)-resident species and marine juvenile migrants is relatively small and only marine seasonal visitors include larger more adult fish (van der Veer et al. 2015, van Walraven et al. 2017). Another factor might be area-specific differences in feeding pattern or in contribution of different items to the diet for both (near)-resident species and marine juvenile migrants. For instance, *Pomatischistus minutus*, a (near)-resident species, mainly consumes *Corophium volutator* in Swedish bays (Pihl 1985) and small *Crangon crangon* in the Dutch Wadden Sea (Kühl & Kuipers 1983).

Also, for marine juvenile migrants differences occur. 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 are (near)-resident species, marine juvenile migrants and marine seasonal visitors. The trophic position of the (near)-resident species covers a range from 3.2 to 4.7, meaning that these (near)-resident species are more secondary consumers (carnivores) and tertiary consumers (carnivores consuming other carnivores). The marine juvenile migrants cover a narrow range in trophic position from 3.2 to 3.4, reflecting that these juvenile fish are not tertiary consumers. Marine seasonal visitors cover the largest range from 2.4 to 4.7. They include herbivore species up to tertiary consumers.

The trophic positions of the present fish community illustrate that the trophic structure still covers the various levels up to tertiary consumers, despite the disappearance 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 through loss of trophic positions but rather strong reductions in abundance of a various trophic positions due to the great 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 marine juvenile migrants in autumn compared to spring.

4.2. Food web structure

Stomach content analysis shows that all species are consuming multiple preys indicating 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 content support this, with clustering 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 [1] feeders on minute particles from the bottom; [2] zooplankton feeders; [3] zoobenthos feeders and [4] fish feeders.

Notably, (near)-resident species and marine seasonal visitors show 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 nowadays than in the past.

Marine juvenile 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 areas is mainly a conversion of energy: the energy influx of the massive amounts of marine juvenile migrant larvae is in 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 by many fish species and thereby form important links in the fish food web. Juvenile herring form a link of the plankton to the secondary consumers by their consumption of copepods (Last 1989); while brown shrimps by their consumption of (epi)benthic prey items (Wolff & Zijlstra 1983, Pihl & Rosenberg 1984) link the benthos to the secondary consumers. Copepods, brown shrimps and mysid shrimps were also the most abundant prey items of the 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, however 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 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 (micro-phytobenthos) are the most important energy source for the majority of consumers of 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 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) has argued that in the past before exploitation started in general fish populations might have been determined by resource limitation. Anecdotic information indicates that fish biomass in the Wadden Sea has been substantially higher in the past even allowing a community of fisherman a living with passive fyke nets until it came to an end in about the 1960-ties due to decreasing catches. This did not stop a further decrease in fish abundance in the area especially from the 1980ties 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 being 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 and 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 a few abundant species only, especially juvenile herring and brown shrimps that are the most preferred prey items by many 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 (McCall 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 marine juvenile 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, the sand goby *Pomatoschistus minutus*, indicated that growth was not food-limited (Freitas et al 2011), suggesting the absence of such a bottom-up control. For some marine juvenile migrants, 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 holds also true for pelagic marine juvenile species (herring, sprat) and (near)-resident is unclear. It cannot be excluded that control is not linked to latitude (temperature) as suggested by Frank et al. (2007) but also on feeding guild, whereby especially zooplankton feeders such as herring (marine juvenile migrants) and fish feeders (such as much of the marine seasonal visitors) are more sensitive for bottom-up control.

A food web that depends on a 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 input (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 a middle trophic position passes most of the energy to higher predators.

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5. References

Baker R, Buckland A, Sheaves M (2014) Fish gut content analysis: robust measures of diet composition. Fish Fish 15:170-177

Cardoso JFMF, Freitas V, Quilez I, Jouta J, Witte JIJ, van der Veer HW (2015) The European sea bass *Dicentrarchus labrax* in the Dutch Wadden Sea: from visitor to resident species. J Mar Biol Assoc UK 95:839–850

Chevillot X, Tecchio S, Chaalali A, Lassalle G, Selleslagh J, Castelnaud G, David V, Bachelet G, Niquil N, Sautour B, Lobry J (2019) Global changes jeopardize the trophic carrying capacity and functioning of estuarine ecosystems. Ecosystems 22:473–495

Christianen MJA, Middelburg JJ, Holthuijsen SJ, Jouta J, Compton TJ, van der Heide T, Sinninghe Damste JSS, Piersma T, van der Veer H.W, Schouten S, Olff H (2017) Benthic primary producers are key to sustain the Wadden Sea food web: a stable isotope analysis at landscape scale. Ecology 98:1498-1512

Cloern JE, Foster SQ, Kleckner AE (2014) Phytoplankton primary production in the world's estuarine-coastal ecosystems. Biogeosciences 11:2477–2501

Day L, Le Bris H, Saulnier E, Pinsivy L, Brind'Amour A (2020) Benthic prey production index estimated from trawl survey supports the food limitation hypothesis in coastal fish nurseries Estuar Coast Shelf Sci 235:106594 de Jonge VN (1990) Response of the Dutch Wadden Sea ecosystem to phosphorus discharges from the River Rhine. Hydrobiologia, 195:49-62

de Jonge VN, Postma H (1974) Phosphorus compounds in the Dutch Wadden Sea. Neth J Sea Res 8:139-153

de Vlas J (1979) Annual food intake by plaice and flounder in a tidal flat area in the Dutch Wadden Sea, with special reference to consumption of regenerating parts of macrobenthic prey. Neth J Sea Res 13:117–153

de Wilde, PAWJ, Beukema JJ (1984) The role of the zoobenthos in the consumption of organic matter in the Dutch Wadden Sea. Publ Ser Neth Inst Sea Res 10:145–158

Daan N (1973) A quantitative analysis of the food intake of North Sea cod, *Gadus morhua*. Neth J Sea Res 6:479-517

Deegan L, Garritt R (1997) Evidence for spatial variability in estuarine food webs. Mar Ecol Prog Ser 147:31–47

Elliott M, Dewailly F (1995) The structure and components of European estuarine fish assemblages. Neth J Aquat Ecol 29:397–417

Evans S (1984) Energy budgets and predation impact of dominant epibenthic carnivores on a shallow soft bottom community at the Swedish west coast. Estuar Coast Shelf Sci 18:651–672

Frank KT, Petrie B, Shackell NL (2007) The ups and downs of trophic control in continental shelf ecosystems. TREE 22:236-242

Freitas V, Campos J, Fonds M, van der Veer HW (2007) Potential impact of temperature change on epibenthic predator–bivalve prey interactions in temperate estuaries. J Therm Biol 32:328–340

Freitas V, Campos J, Skreslet S, van der Veer HW (2010) Habitat quality of a subarctic nursery ground for 0-group plaice (*Pleuronectes platessa* L.). J Sea Res 64:26–33

Freitas V, Lika K, Witte JIJ, van der Veer HW (2011) Food conditions of the sand goby *Pomatoschistus minutus* in shallow waters: an analysis in the context of Dynamic Energy Budget theory. J Sea Res 66:440-446

Froese R, Pauley D (2019) FishBase. www.fishbase.org.

Gibson RN (1994) Impact of habitat quality and quantity on the recruitment of juvenile flatfishes. Neth J Sea Res 32:191–206

Goodall DW (1983) Estuaries and enclosed seas, 26th ed. Elsevier Scientific Pub. Co., Amsterdam

Hayward PJ, Ryland JS (2017) Handbook of the marine fauna of North-West Europe. Oxford University Press, 740 pp

Hynes HBN (1950) The food of the freshwater sticklebacks (*Gastrosteus aculeatus* and *Pygosteus pungitius*) with a review of methods used in studies of the food of fishes. J Anim Ecol 19:36–58

Jones R (1989) Towards a theory of population regulation in marine teleosts. J Cons int Explor Mer 45:176-189

Jung AS, Dekker R, Germain M, Philippart CJM, Witte JIJ, van der Veer HW (2017) Long-term shifts in intertidal predator and prey communities in the Wadden Sea and consequences for food requirements and supply. Mar Ecol Prog Ser 579:37–53

Jung AS, van der Veer HW, van der Meer MTJ, Philippart CJM (2019) Seasonal variation in the diet of estuarine bivalves. PLoS One 14:e0217003

Kellnreiter F, Pockberger M, Asmus H (2012) Seasonal variation of assemblage and feeding guild structure of fish species in a boreal tidal basin. Estua Coast Shelf Sci 108:97-108

Kühl H (1961) Nahrungsuntersuchungen an einigen Fischen im Elbe-Mündungsgebiet. Ber Dt wiss Komm Meeresforsch 16:90-104

Kühl H (1973) Nahrungsuntersuchungen an einigen Gadiden im Elbe-Mündungsgebiet. Arch Fisch Wiss 24:141-149

Kühl H, Kuipers BR (1983) Qualitative food relationships of Wadden Sea fishes. In: Wolff, WJ (Ed) Ecology of the Wadden Sea Balkema Press 5/122-5/123

Kuipers BR (1977) On the ecology of juvenile plaice on a tidal flat in the Wadden Sea. Neth J Sea Res 11:56-91

Kuipers BR, de Wilde PAWJ, Creutzberg F (1981) Energy flow in a tidal flat ecosystem. Mar Ecol Prog Ser 5:215–221

Last JM (1989) The food of herring, *Clupea harengus*, in the North Sea, 1983-1986. J Fish Biol 34:489-501

Levin LA, Etter RJ, Rex MA, Gooday AJ, Smith CR, Pineda J, Stuart CT, Hessler RR, Pawson D (2001) Environmental influences on regional deep-sea species diversity. Ann Rev Ecol Syst 32:51–93

Lotze HK (2007) Rise and fall of fishing and marine resource use in the Wadden Sea, southern North Sea. Fish Res 87:208–218

McCall AD (1990) Dynamic geography of marine fish populations. University of Washington Press, Seattle. 153 pp

Mulas A, Bellodi A, Cannas R, Cau A, Cuccu D, Marongiu MF, Porcu C, Follesa MC (2015) Diet and feeding behaviour of longnosed skate *Dipturus oxyrinchus*. J Fish Biol 86:121–138

Nash RDM, Geffen AJ, Burrows MT, Gibson RN (2007) Dynamics of shallow-water juvenile flatfish nursery grounds: application of the self-thinning rule. Mar Ecol Prog Ser 344: 231-244

Nijssen H (2001) Veldgids Zeevissen. Koninklijke Nederlandse Natuurhistorische Vereniging (KNNV). Utrecht 160-168

Nixon SW (1995) Coastal marine eutrophication: A definition, social causes, and future concerns. Ophelia 41:199–219

Norte-Campos, AGC, Temming A (1994) Daily activity, feeding and rations in gobies and brown shrimp in the northern Wadden Sea. Mar Ecol Prog Ser 115:41-53

Pihl L, Rosenberg R (1984) Food selection and consumption of the shrimp *Crangon crangon* in some shallow marine areas in western Sweden. Mar Ecol Prog Ser 15:159-168

Pihl L (1985) Food selection and consumption of mobile epibenthic fauna in shallow marine areas. Mar Ecol Prog Ser 22:169-179

R Core Team (2019) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/

Rice J (1995) Food web theory, marine food webs, and what climate may change may do to northern marine fish populations. In: Beamish (Ed) Climate change and northern fish populations. Can Spec Publ Fish Aquat Sci 121:561-568

Saulnier E, Le Bris H, Tableau A, Dauvin JC, Brind'Amour A (2020) Food limitation of juvenile marine fish in a coastal and estuarine nursery. Estua Coast Shelf Sci 241: 106670

Tulp I, Bolle LJ, Rijnsdorp AD (2008) Signals from the shallows: In search of common patterns in long-term trends in Dutch estuarine and coastal fish. J Sea Res 60:54–73

Tulp I, van der Veer HW, Walker PA, van Walraven L, Bolle LJ (2017) Can guild- or site-specific contrasts in trends or phenology explain the changed role of the Dutch Wadden Sea for fish? J Sea Res 127:150-163

Ursin E (1973) On the prey size preferences of cod and dab. Meddr Danm Fisk- og Havunders NS 7:85-98

van der Veer HW, Witte JIJ (1993) The 'maximum growth/optimal food condition' hypothesis, a test for 0-group plaice *Pleuronectes platessa* in the Dutch Wadden Sea. Mar Ecol Prog Ser 101:81-90

van der Veer HW, Berghahn R, Miller JM, Rijnsdorp AD (2000) Recruitment in flatfish, with special emphasis on North Atlantic species: progress made by the Flatfish Symposia. ICES J Mar Sci 57:202-215

van der Veer HW, Koot J, Aarts G, Dekker R, Diderich W, Freitas V, Witte, JIJ (2011) Long-term trends in juvenile flatfish indicate a dramatic reduction in nursery function of the Balgzand intertidal, Dutch Wadden Sea. Mar Ecol Prog Ser 434:143-154

van der Veer HW, Dapper R, Henderson PA, Jung AS, Philippart CJM, Witte JIJ, Zuur AF (2015) Changes over 50 years in fish fauna of a temperate coastal sea: Degradation of trophic structure and nursery function. Estua Coast Shelf Sci 155:156–166

van Walraven L, Dapper R, Nauw JJ, Tulp I, Witte JIJ, van der Veer HW (2017) Long-term patterns in fish phenology in the western Dutch Wadden Sea in relation to climate change. J Sea Res 127:173–181

Wheeler A (1978) The fishes of the British Isles and North-West Europe. Frederick Warne, London, 380 pp

Wickham H (2009) Ggplot2. Springer New York, New York, NY

Witte JIJ, Zijlstra JJ (1983) The species of fish occurring in the Wadden Sea. In: Wolff WJ (Ed) Ecology of the Wadden Sea. Balkema, Rotterdam, The Netherlands. 5/10-5/19

Wolff WJ (1980) Biotic aspects of the chemistry of estuaries. In: Olausson E, Cato I (Eds.) Chemistry and biogeochemistry of estuaries. John Wiley & Sons:264-295

Wolff WJ (1983) Ecology of the Wadden Sea. Balkema, Rotterdam, The Netherlands

Wolff WJ (2000) Causes of extirpations in the Wadden Sea, an estuarine area in the Netherlands. Conserv Biol 14:876–885

Wolff WJ, Zijlstra JJ (1983) The common brown shrimp *Crangon crangon*. In: Wolff WJ (Ed) Ecology of the Wadden Sea. Balkema, Rotterdam, The Netherlands. 4/122-4/123

Zijlstra JJ (1972) On the importance of the Wadden Sea as a nursery area in relation to the conservation of the southern North Sea fishery resources. Symp Zool Soc Lond 29:233–258

Zijlstra JJ (1983) The function of the Wadden Sea for the members of its fish-fauna. In: Wolff WJ (Ed) Ecology of the Wadden Sea. Balkema, Rotterdam, The Netherlands. 5/20-5/26

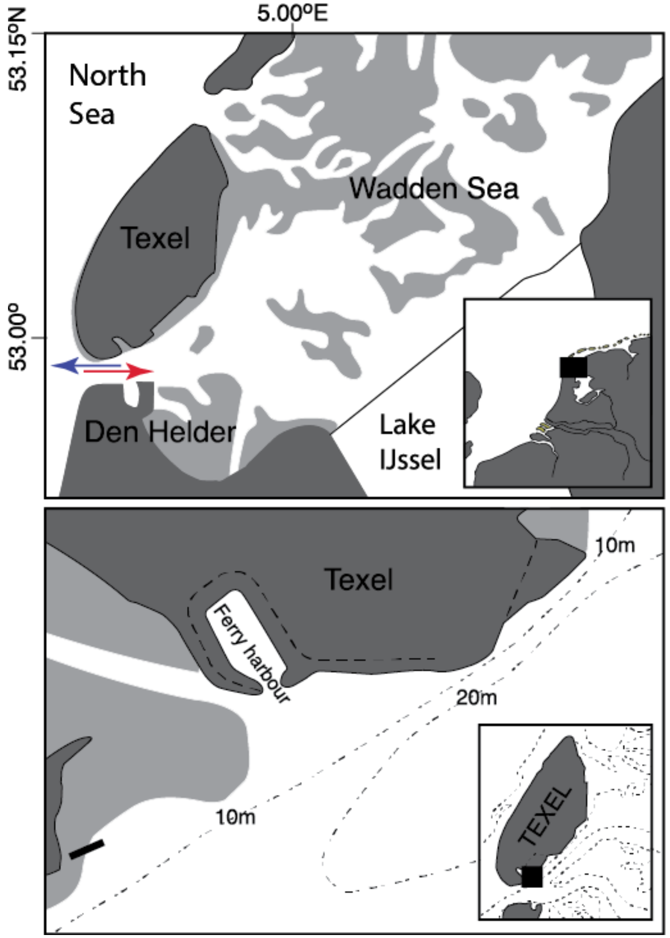

Figure 1 Sampling location near the island of Texel. Top panel: western Dutch Wadden Sea (black box); red arrow indicates inwards migration in spring and blue arrow outward migration in autumn. Lower panel: fyke net position (black bar). Grey: intertidal areas.

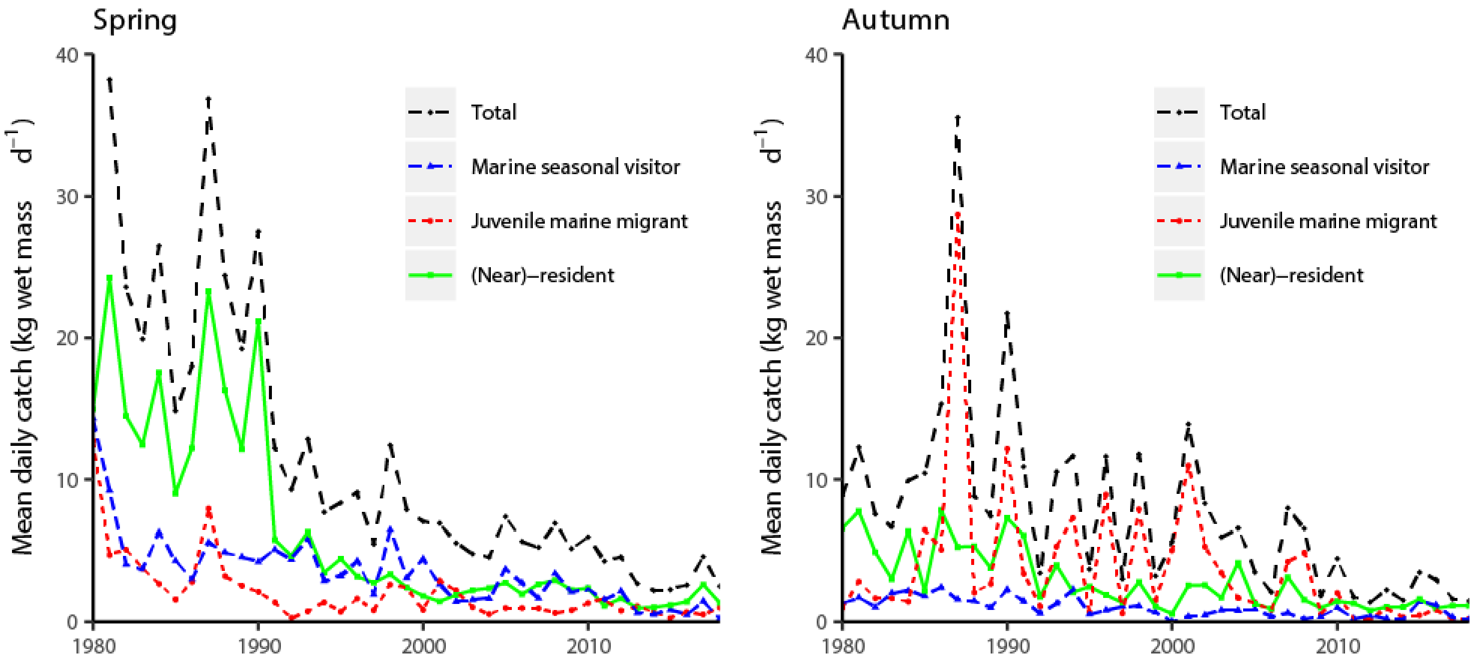

Figure 2 Mean daily fyke catch (kg wet mass d^{-1}), total and for the different groups in spring (upper panel) and autumn (lower panel).

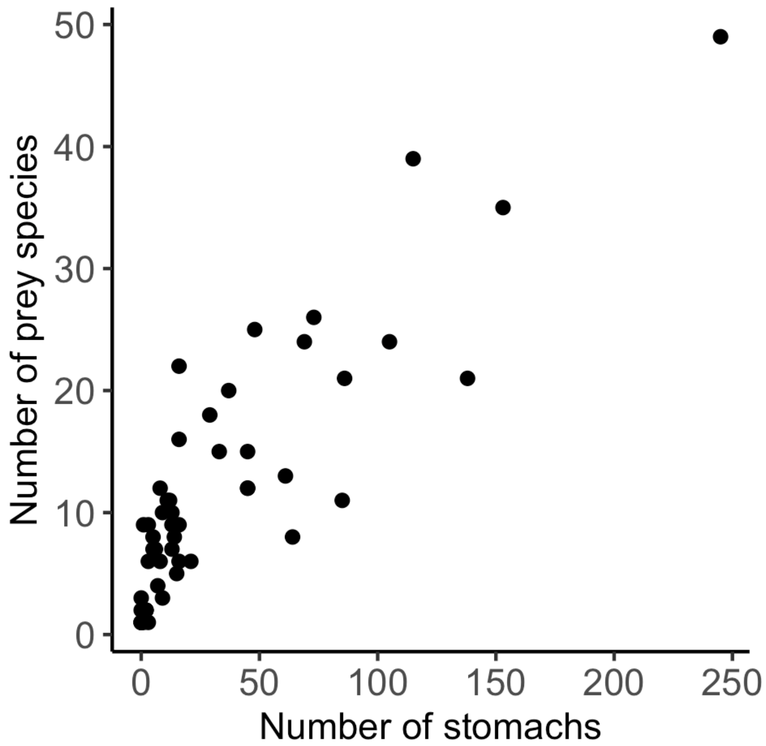

Figure 3 Number of stomachs analyzed for each fish species compared in relation to the total number of different prey species found inside those stomachs. All years combined (2010 – 2018).

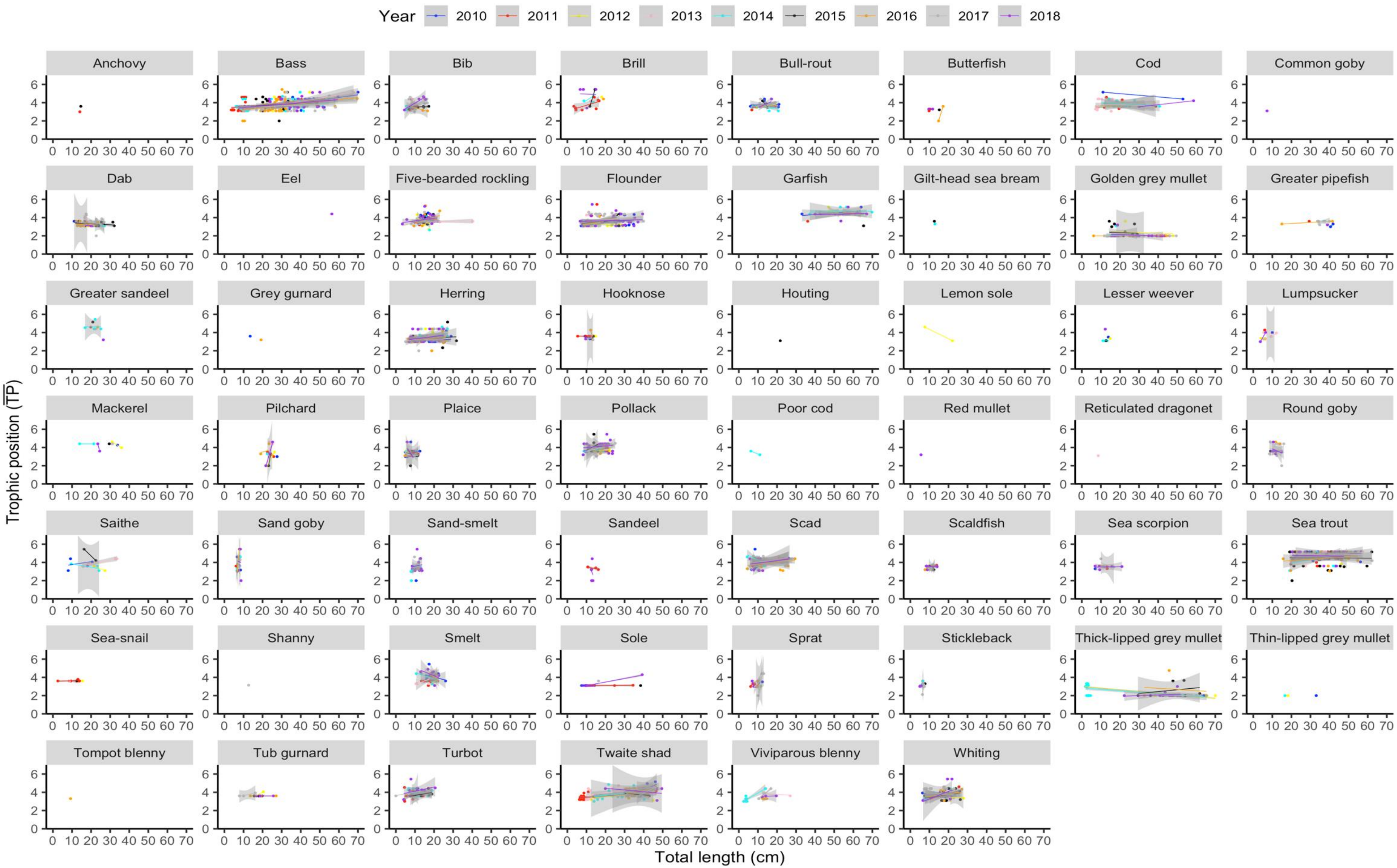

Figure 4 Calculated trophic positions ($\overline{TP}$) based on the stomach content as a function of the total length for each predatory species. A linear regression with a 95% confidence interval for each year (2010 -2018) is added to visualize trends.

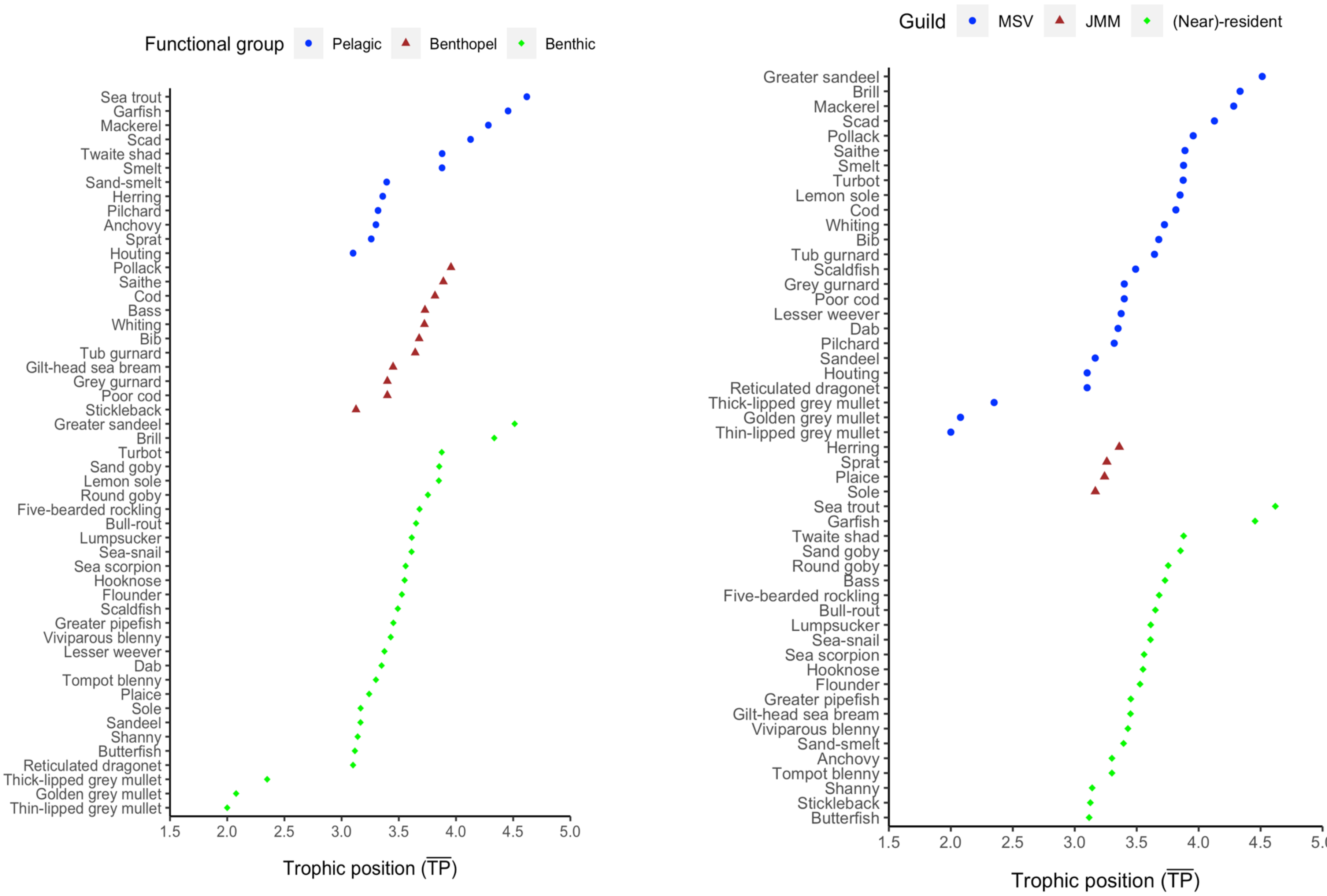

Figure 5 Trophic position ($\overline{TP}$) of the fish species based on stomach content analysis. divided into the functional groups (left panel. with blue: pelagic. green: benthopelagic and brown: demersal/benthopelagic species) and into species guild (right panel. blue: marine seasonal visitors (MSV). green: (near)-residents and brown: juvenile marine migrants (JMM). Species are listed from lowest TP to highest TP.

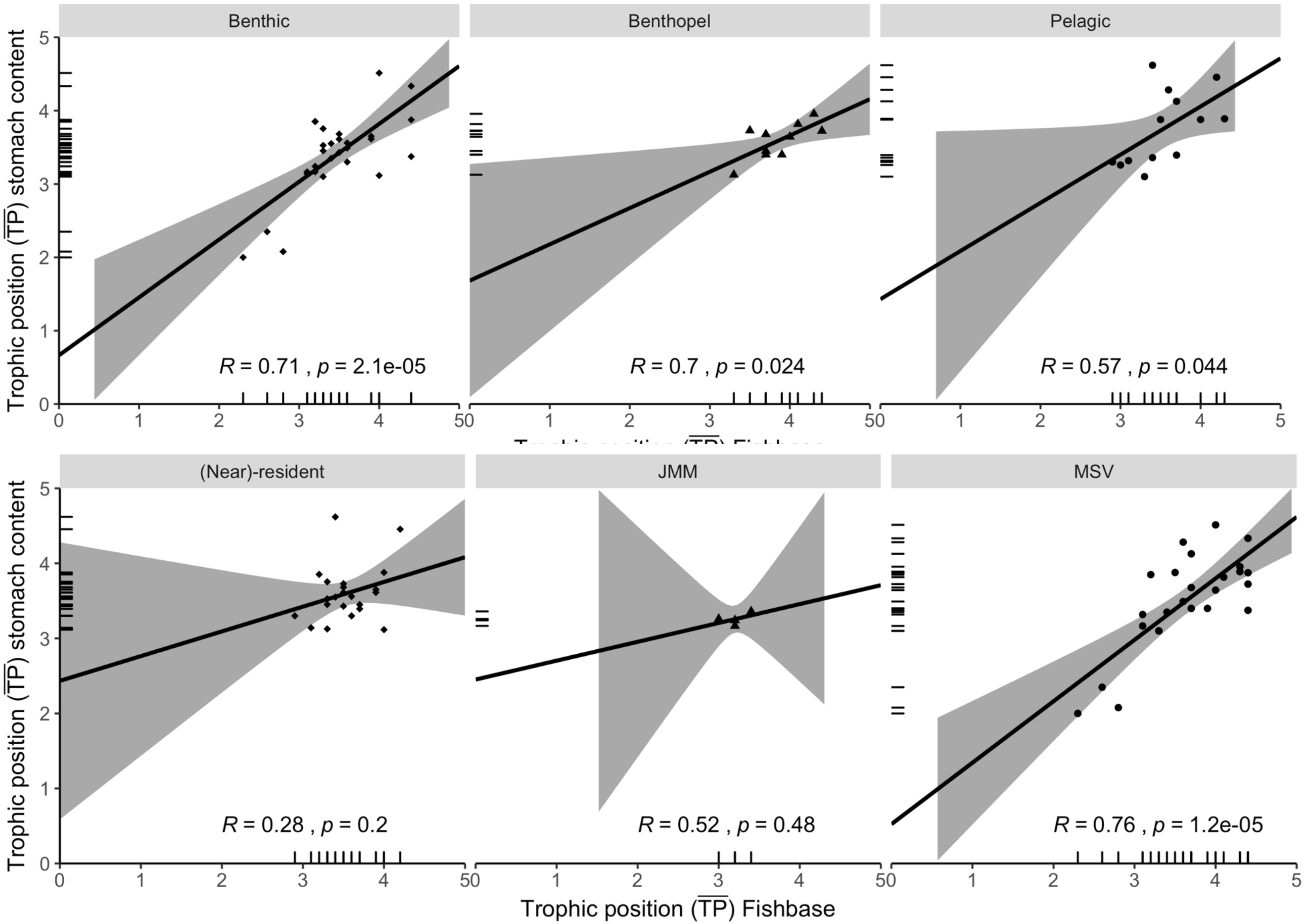

Figure 6 Linear relationship with 95% confidence interval between trophic position ($\overline{TP}$) from FishBase and the trophic position ($\overline{TP}$) based on the stomach content analysis. Upper panel for the various functional group. Lower panel for the various guild.

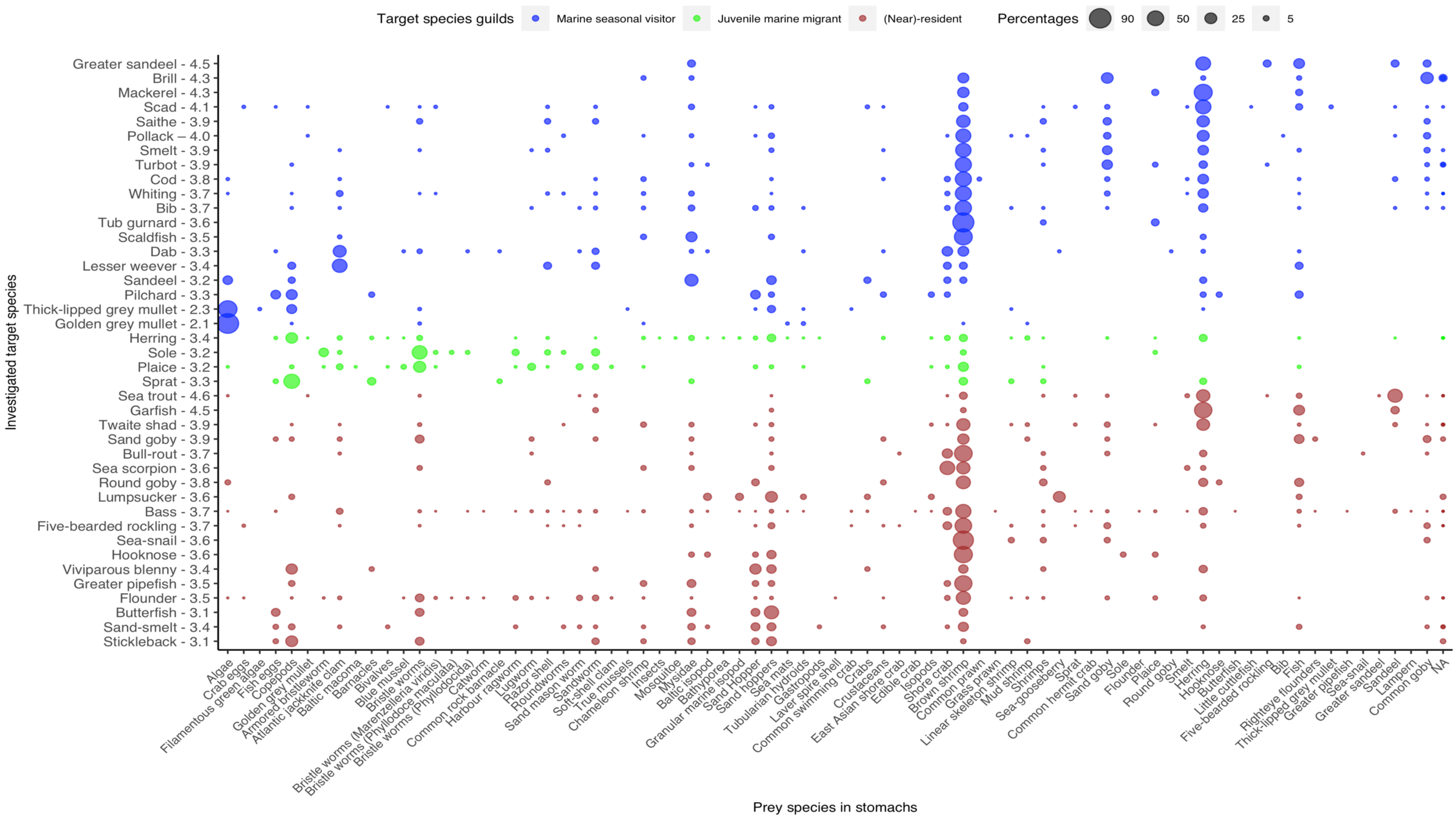

Figure 7 Occurrence of prey species (%) in the stomach of fish species in the years 2010 – 2018 together with corresponding calculated trophic position (TP) and guild. Predatory fish species are listed from guild type and lowest TP to highest TP and prey species are listen from lowest TP to highest TP.

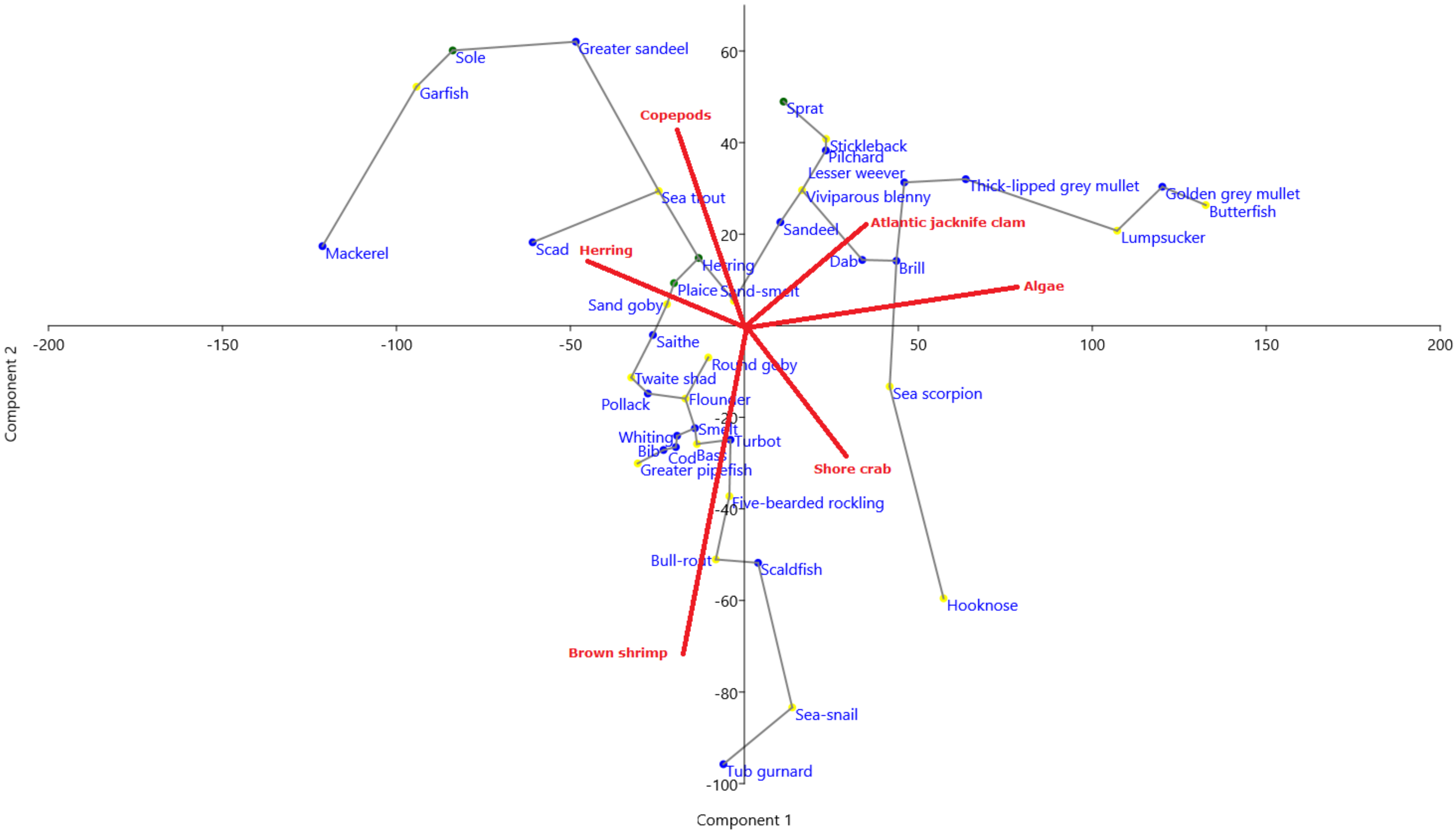

Figure 8 Principal Component Analysis (PCA) per species for each guild based on the stomach content. Yellow: (near)-residents. blue: marine seasonal visitor and green: juvenile marine migrant. The PCA illustrates the clustering around algae, copepods, brown shrimps and herring.

Supplementary information

Table S1. General information of species analysed.

Species	SpeciesLatin	TP calculated by stomach content	TP according to FishBase	Functional group	Guild
Anchovy	*Engraulis encrasicolus*	3,3	2,9	Pelagic	(Near)-resident
Bass	*Dicentrarchus labrax*	3,7	3,5	Benthic	(Near)-resident
Bib	*Trisopterus luscus*	3,7	3,7	Benthopelagicpelagic	MSV
Brill	*Scophthalmus rhombus*	4,3	4,4	Benthic	MSV
Bull-rout	*Myoxocephalus scorpius*	3,7	3,9	Benthic	(Near)-resident
Butterfish	*Pholis gunellus*	3,1	4	Benthic	(Near)-resident
Cod	*Gadus morhua*	3,8	4,1	Benthopelagic	MSV
Dab	*Limanda limanda*	3,3	3,4	Benthic	MSV
Five-bearded rockling	*Ciliata mustela*	3,7	3,5	Benthic	(Near)-resident
Flounder	*Platichthys flesus*	3,5	3,3	Benthic	(Near)-resident
Garfish	*Belone belone*	4,5	4,2	Pelagic	(Near)-resident
Gilt-head sea bream	*Spanus aurata*	3,5	3,7	Benthopelagic	(Near)-resident
Golden grey mullet	*Chelon aurata*	2,1	2,8	Benthic	MSV
Greater pipefish	*Syngnathus acus*	3,5	3,3	Benthic	(Near)-resident
Greater sandeel	*Hyperoplus lanceolatus*	4,5	4	Benthic	MSV
Grey gurnard	*Eutrigla gurnardus*	3,4	3,9	Benthopelagic	MSV
Herring	*Clupea harengus*	3,4	3,4	Pelagic	JMM
Hooknose	*Agonus cataphractus*	3,6	3,4	Benthic	(Near)-resident
Houting	*Coregonus oxyrinchus*	3,1	3,3	Pelagic	MSV
Lemon sole	*Microstomus kitt*	3,9	3,2	Benthic	MSV
Lesser weever	*Echeiichthys vipera*	3,4	4,4	Benthic	MSV
Lumpsucker	*Cyclopterus lumpus*	3,6	3,9	Benthic	(Near)-resident

Mackerel	*Scomber scombrus*	4,3	3,6	Pelagic	MSV
Pilchard	*Sardine pilchardus*	3,3	3,1	Pelagic	MSV
Plaice	*Pleuronectes platessa*	3,2	3,2	Benthic	JMM
Pollack	*Pollachius pollachius*	4,0	4,3	Benthopelagic	MSV
Poor cod	*Trisopterus minutus*	3,4	3,7	Benthopelagic	MSV
Reticulated dragonet	*Callionymus reticulatus*	3,1	3,3	Benthic	MSV
Round goby	*Neogobius melanostomus*	3,8	3,3	Benthic	(Near)-resident
Saithe	*Pollachius virens*	3,9	4,3	Pelagic	MSV
Sand goby	*Pomatoschistus minutus*	3,9	3,2	Benthic	(Near)-resident
Sand-smelt	*Atherina presbyter*	3,4	3,7	Pelagic	(Near)-resident
Sandeel	*Ammodytes tobianus*	3,2	3,1	Benthic	MSV
Scad	*Alosa alosa*	4,1	3,7	Pelagic	MSV
Scaldfish	*Arnoglossus laterna*	3,5	3,6	Benthic	MSV
Sea scorpion	*Taurulus bubalis*	3,6	3,6	Benthic	(Near)-resident
Sea trout	*Salmo trutta*	4,6	3,4	Pelagic	(Near)-resident
Sea-snail	*Liparis liparis*	3,6	3,5	Benthic	(Near)-resident
Shanny	*Lipophrys pholis*	3,1	3,1	Benthic	(Near)-resident
Smelt	*Osmerus eperlanus*	3,9	3,5	Pelagic	MSV
Sole	*Solea solea*	3,2	3,2	Benthic	JMM
Sprat	*Sprattus sprattus*	3,3	3	Pelagic	JMM
Stickleback	*Gasterosteus aculeatus*	3,1	3,3	Benthopelagic	(Near)-resident
Thick-lipped grey mullet	*Chelon labrosus*	2,3	2,6	Benthic	MSV
Thin-lipped grey mullet	*Chelon ramada*	2,0	2,3	Benthic	MSV
Tompot blenny	*Parablennius gattorugine*	3,3	3,6	Benthic	(Near)-resident
Tub gurnard	*Chelidonichthys lucerna*	3,6	4	Benthopelagic	MSV
Turbot	*Scophthalmus maxima*	3,9	4,4	Benthic	MSV
Twaite shad	*Alosa fallax*	3,9	4	Pelagic	(Near)-resident

Viviparous blenny	*Zoarces viviparus*	3,4	3,5	Benthic	(Near)-resident
Whiting	*Merlangus merlangus*	3,7	4,4	Benthopelagic	MSV