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Stomach content analysis indicates multi decadal trophic stability in a temperate coastal fish food web, western Dutch Wadden Sea

Suzanne S.H. Poiesz [a,b,*], Johannes IJ. Witte [a], Henk W. van der Veer [a]

[a] NIOZ Royal Netherlands Institute for Sea Research, Department of Coastal Systems, P.O. Box 59, 1790, AB, Den Burg, Texel, the Netherlands
[b] Faculty of Science and Engineering, Groningen Institute of Evolutionary Life Sciences, University of Groningen, P.O. Box 11103, 9700, CC, Groningen, the Netherlands

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ABSTRACT

Information about stomach content composition of fish species of a temperate coastal fish community (western Dutch Wadden Sea) over the period 1930–2019 was analysed to reconstruct long-term trends in trophic position of individual species. Stomach data were not evenly distributed but clustered both with respect to years as well as fish species. For 18 fish species, all being omnivorous and belonging to different functional groups (pelagic, benthopelagic, demersal) and guilds [(near)-resident, juvenile marine migrants, marine seasonal visitiors], prey consumption and trophic position over time could be analysed. Prey occurrence in the stomachs of different fish species showed variability over time, most likely due to fluctuations in prey abundance, but without a trend. For all species, individual fish showed variablity in trophic position in the order of 1 unit or even more both within and between years. However, in all 18 species, no significant trend in mean trophic position over time could be found, despite the serious anthropogenic stress (pollution, eutrophication events, climate change) and the decrease in fish abundance in the area during the last 50 years. The present study does not indicate any changes in trophic position of individual species in the western Dutch Wadden Sea over the last 80 years. At the community level, trophic structure varies due to interannual fluctuations in species composition and year-to year fluctuations in the relative abundance of the various fish species. At the ecosystem level the trophic role of the fish community has been degraded due to the decrease in total fish biomass in the area.

1. Introduction

Coastal systems provide a large variety of ecosystem goods and services (see Barbier, 2017; Liu et al., 2021) and consequently, their ecosystem value is high (Liu et al., 2021). Coastal systems are known as important foraging grounds for a variety of fish, bird and marine mammal species (e.g. Goodall, 1983; Beck et al., 2001), and in these areas fish harvesting has been an important marine ecosystem good for centuries. However, due to human fishing and hunting, coastal ecosystems have also been under pervasive human disturbance for centuries (Jackson et al., 2001; Lotze, 2007). For the future, anthropogenic pressure in these areas is expected to continue especially due to the combined pressure of overfishing and habitat destruction, pollution and climate change (Bijma et al., 2013; European Marine Board, 2013).

Predicting the consequences of the still ongoing threats on the future productivity of coastal areas requires (among other factors) insight into the food web structure of these systems. The fact that coastal ecosystems have been under pervasive human disturbance already for centuries makes it difficult to get insight in their 'original pristine state' and to assess the impact of human disturbance over time. First of all, going back in time, information about ecosystem status becomes more and more qualitative and anecdotic. Furthermore, our perspective about the past also suffers from "the shifting baseline phenomenon": ecosystem changes are considered relative to the situation the evaluator can remember and therefore the baseline shifts with each generation (Pauly, 1995; Zeller et al., 2005). This stresses the need for long time series of reliable information on ecosystem structure, preferably covering multiple observer generations. In this study, we focus on the fish food web in the international Wadden Sea, one of the largest estuarine areas in the world, bordering the Dutch, German and Danish North Sea coast. The area is an important resting and fuelling area for birds and nursery area for various (non)commercial fish species (Zijlstra, 1972; Wolff, 1983). From archaeological, historical, fisheries, and ecological records, it is clear that the Wadden Sea have been under pervasive disturbance for

* Corresponding author. NIOZ Royal Netherlands Institute for Sea Research, Department of Coastal Systems, P.O. Box 59, 1790, AB, Den Burg, Texel, the Netherlands.

E-mail address: suzannepoiesz@gmail.com (S.S.H. Poiesz).

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centuries already (Lotze, 2005, 2007).

Quality status reports about the ecology of the Wadden Sea has been produced periodically since 1999 (https://qsr.waddensea-worldheritage.org), with various ecological monitoring series in the western part of the area on phytoplankton (Philippart et al., 2007; Jacobs et al., 2020), macrozoobenthos (Beukema and Dekker, 2020) and fish (Tulp et al., 2008; van der Veer et al., 2015) providing reconstructions over the last 60 years. From the 1970's, no changes in fish biodiversity was found. However, fish abundance of both pelagic and demersal species showed a 10-fold decrease in catches from 1980s onwards (Tulp et al., 2008; van der Veer et al., 2015). At present, various stomach content studies show that most Wadden Sea fish species are omnivorous, feeding on multiple prey items with a pivotal position of a few key prey species (Kellnreiter et al., 2012; Whitehouse et al., 2017; Poiesz et al., 2020, 2023). Stable isotope analyses indicates that the fish food web in this area consists of a spatially stable structure with various trophic levels (Poiesz et al., 2021a, 2023). To what extend the decrease in fish abundance in the 1980s has caused a shift in prey selection and therefore a temporal change in their trophic positions by the omnivorous predatory fish species, is unclear.

Ecological information about the fish food web before the 1970's is mostly qualitative and anecdotic, except for stomach content information of the fish fauna as a by-product of the long-lasting human fishing in the area. Stomach content data is an important source of information (Kellnreiter et al., 2012; Whitehouse et al., 2017; Poiesz et al., 2020), despite the fact that it is labour intensive, requires taxonomic expertise and only offers a small temporal snapshot of recently consumed prey items and might thus be sensitive to sampling design (Poiesz et al., 2023). In the absence of stable isotope information, stomach content information can be used to derive trophic structure of the fish fauna and its predator−prey interactions (Hynes, 1950; Baker et al., 2014; Poiesz et al., 2020, 2021). A recent comparison of stomach content information and stable isotopes of fish in the western Wadden Sea, illustrated that both resulted in a similar picture of the trophic structure of the fish fauna (Poiesz et al., 2023).

For long-term stomach content time series, standardised methods of sampling and analysis are important (see for overview Hyslop, 1980; Buckland et al., 2017; Amundsen and Sánchez-Hernández, 2019). However, time series often suffer from limitations due to differences over time in sampling strategy, sampling intensity and/or in detail and methods of the analyses. In case enough data are present General Additive Models (GAMs) can be applied to visualise and analyse trends in stomach content over time (Hastie and Tibshirani, 1995; Kvaarik et al., 2019; Kordubel et al., 2024). In this study we focus on unpublished records of fish stomach content data, mainly from the western part of Wadden Sea form the NIOZ archive, dating back to the 1930's (de Vooys et al., 1991, 1993). For all species, missing observations and/or gaps in the time series occurred. Furthermore, not all records contained information about number of prey found, prey condition, and prey weight. Therefore, Buckland et al. (2017) was followed and the simple presence/absence and frequency of occurrence approach was taken, since it is not affected by prey condition and hence provides a rapid, unambiguous and reliable account of diet composition and prey trophic position.

This NIOZ archive stomach content information is used to analyse fluctuations in predator-prey relationships and in the trophic position of individual fish species over the last century with the aim to get insight in the temporal variability of the Wadden Sea fish food web. The present trophic position of the various fish species (Poiesz et al., 2020, 2021a) will be used as reference to test whether shifts in trophic position of individual fish species has occurred over time. The stomach content data are available for the time span 1930 – present and thus the time series period covers more than a single scientific career. As such, the results of this study can also be used to correct for the "shifting baseline phenomenon".

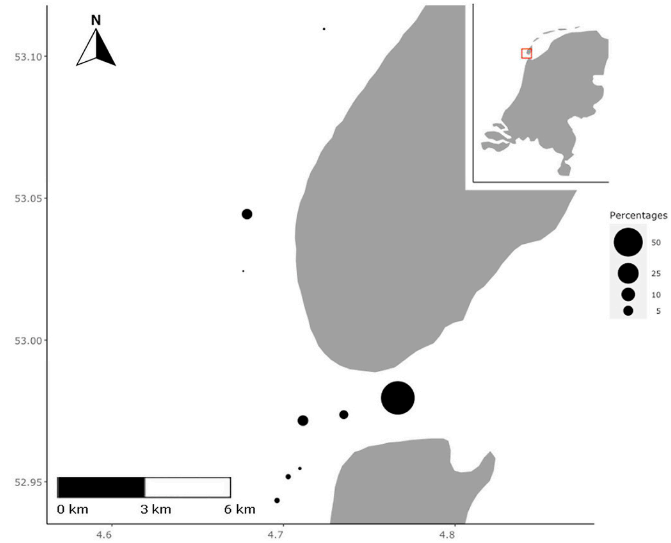

Fig. 1. Sampling locations from the North Sea coast and Wadden Sea. Size of black dots indicate the contribution (%) in the amount of individuals caught for each sampling location.

2. Material and methods

2.1. Data collection

From 1930 onwards the Royal Netherlands Institute for Sea Research (NIOZ) registered observations and landings of fish and invertebrate species from the western Wadden Sea and nearby Dutch coastal waters (Fig. 1). Most information originated from NIOZ cruises and fish collected during NIOZ courses. In addition landings of rare fish species from fishermen were recorded. All individual fish were identified and information about species and stomach content was recorded. From the beginning, data collection, section and stomach content analysis was done by specialised NIOZ personnel only. A more detailed description of the NIOZ archive can be found in de Vooys et al. (1991, 1993).

From the 1980's onwards, stomach content data were collected from a long-term monitoring programme of the fish fauna with a passive fish trap near the entrance of the Wadden Sea in spring and autumn (Poiesz et al., 2020). Until 2010, all fish caught on Fridays were taken to the laboratory and sorted within an hour, identified up to species level, counted and length measured. From 2017 onwards, a maximum of three individuals per species per week were selected and stored at −20 °C for further analysis. Within a month, individuals were defrosted, and stomach content was taken out and analysed in a Petri dish under a binocular (20x). Of each individual fish, total stomach content was determined (wet mass; g) and subsequently, prey items were identified up to species level or sometimes, 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 *Alitta virens* or *Ensis leei,* or from species that were in parts, such as the *Crangon crangon*, were counted only by the number of 'heads'.

Taxonomic identification was based on an internal reference collection and Hayward and Ryland (2017) for polychaetes, bivalves and crabs and Wheeler (1978) for fish species. For more details see van der Veer et al. (2015) and Poiesz et al. (2020).

2.2. Data processing

All fish records were checked for species name and, if necessary, updated according to WoRMS (http://www.marinespecies.org). Next, fish species were assigned in line with previous work (van der Veer et al., 2015; Poiesz et al., 2020) into: pelagic (occurring mainly in the water column between 0 and 200 m, not feeding on benthic organisms); benthopelagic (living and/or feeding on or near the bottom, as well as in midwater, between 0 and 200 m) and benthic (living and/or feeding on the bottom) according to FishBase (Froese and Pauly, 2021). Species were also classified according to their use of the area into near-resident and resident species, marine juvenile migrants and seasonal visitors based on Zijlstra (1983). *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).

All prey items found in the stomachs of the fish were checked and scientific name, family, order and class were updated according to WoRMS (http://www.marinespecies.org)

Level of taxonomic identification of prey items was variable over the years, often Class level from 1930 to 1980 versus species level from 1980 onwards. For all prey Classes, Families and species found, trophic position was taken from FishBase (Froese and Pauly, 2021).

Per year, for each fish species, the mean percentage of occurrence (= number of stomachs containing a prey species divided by total number of stomachs with content examined) of each class of prey items was determined as a measure of diet composition following Baker et al. (2014). Furthermore, the trophic position of each individual fish *j* (TP_j) was calculated from the stomach content as the mean trophic position of the different prey species *k* found in a stomach, according to:

$$TP_j = 1 + \frac{\sum TP_k}{k} \qquad [1]$$

where:

TP_j: being the calculated trophic position of the individual fish *j*;
TP_k: the trophic position of prey species *k* in the stomach of fish *j*.
k: the number of different prey species in the stomach of fish *j*.

The bias introduced by not correcting for differences in mass of the various prey items in the stomachs is small (Poiesz et al., 2021a). Next, for each fish species, the mean trophic position per year was calculated.

2.3. Data analysis

The impact of level of detail of prey identification on estimated trophic level of stomach content was analysed for the 2010–2019 data (Poiesz et al., 2020). Estimated trophic levels of the stomach contents based on trophic values of identified prey species were compared with estimates after a rerun with Class values instead of species values.

In all species, missing observations and gaps in the time series occurred. For fish species, with minimum 15 years of observation with at least 5 stomach contents analysed were present to apply General Additive Models (GAMs) to visualise and analyse trends over time (Hastie and Tibshirani, 1995). For these fish species *i*, trends over time in the most common prey items (PO_i) and in mean trophic position (TP_i) were analysed by fitting GAMs using locally weighted least squares regression (LOESS), an identity link function and the Gaussian error distribution according to:

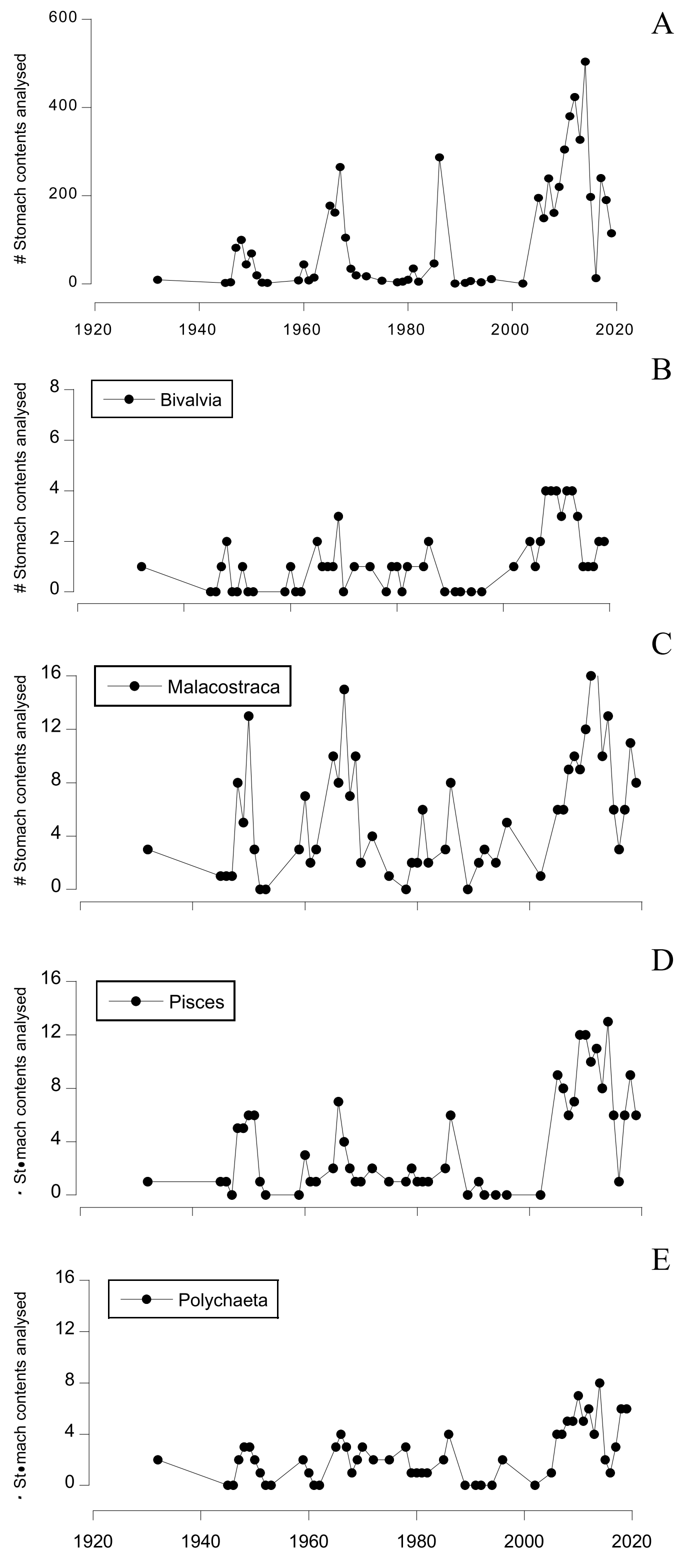

Fig. 2. NIOZ archive.
A: Number of stomachs contents analysed over the years 1932–2019.
B: Number of Bivalve species identified in the Wadden Sea fish stomachs.
C: Number of Malacostraca species identified in the Wadden Sea fish stomachs.
D: Number of Pisces species identified in the Wadden Sea fish stomachs.
E: Number of Polychaete species identified in the Wadden Sea fish stomachs.

Table 1
Overview of prey items found in the stomachs of the various fish species of the NIOZ archive between 1931 and 2019, together with trophic position according to FishBase (www.fishbase.com).

Class	Order	Family	Scientific name	Common name	Trophic position (−)
				Eggs (Crab, shrimp, fish)	1,00
Asteroidea	Forcipulatida	Asteriidae	*Asteriidae*	Sea stars	2,00
Asteroidea	Spatangoida	Loveniidae	*Echinocardium*	Sea urchins	2,00
Bivalvia	Adapedonta			Bivalves	2,10
Bivalvia	Adapedonta	Myridae	*Mya spec*	Solf shell clams	
Bivalvia	Adapedonta	Pharidae	*Ensis*	Razor clams	2,10
Bivalvia	Adapedonta	Pharidae	*Ensis leei*	Atlantic jackknife clam	2,10
Bivalvia	Mytilida	Mytilidae	*Mytilus edulis*	Blue mussel	2,10
Bivalvia	Cardiida	Tellinidae	*Limecola balthica*	Baltic macoma	2,10
Caenogastropoda	Littorinimorpha	Hydrobiidae	*Peringia ulvae*	Laver spire shell	2,40
Chlorophyta	Algae	Algae	*Algae*	Algae	1,00
Chlorophyta	Cladophorales	Cladophoraceae	*Chaetomorpha melagonium*	Chaetomorpha melagonium	1,00
Chlorophyta	Ulvales	Ulvaceae	*Ulva lactuca*	Sea lettuce	1,00
Coleoidea	Cephalopoda	Loliginidae	*Loligo vulgaris*	European squid	3,50
Coleoidea	Cephalopoda	Loliginidae	*Sepia officinalis*	Common cuttlefish	3,50
Coleoidea	Teuthida	Teuthida	*Teuthida*	Squid	3,50
Cydippida	Ctenophora	Ctenophora	*Ctenophora*	Ctenophora	3,00
Cydippida	Cydippida	Pleurobrachiidae	*Pleurobrachia pileus*	Sea-gooseberry	3,00
Discomedusae	Rhizostomeae	Rhizostomatidae	*Rhizostoma pulmo*	Giant jellyfish	3,00
Gastropoda	Littorinimorpha	Littorinimorpha	*Littorinimorpha*	Littorinimorpha	2,40
Heterobranchia	Nudibranchia	Nudibranchia	*Nudibranchia*	Nudibranchs	2,40
Hydrozoa					2,30
Hydrozoa	Anthoathecata	Tubularia	*Tubularia*	Tubularia	2,30
Hydrozoa	Anthoathecata	Corynidae	*Sarsia tubulosa*	Clapper medusa	2,50
Insecta	Insecta	Insecta	*Insecta*	Insects	1,00
Malacostraca	Amphipoda	Isopoda	*Hyperia galba*	Big-eye amphipod	2,30
Malacostraca	Amphipoda	Hyperiidae	*Talitrus saltator*	Sand hopper	2,30
Malacostraca	Amphipoda	Gammaridae	*Gammarus spec*	Gammarus	2,30
Malacostraca	Balanomorpha	Thoracica	*Semibalanus balanoides*	Barnacle	2,10
Malacostraca	Balanomorpha	Thoracica	*Thoracica*	Barnacles	2,30
Malacostraca	Copepoda	Copepoda	*Copepoda*	Copepods	2,00
Malacostraca	Decapoda	Anomura	*Paguroidea*	Hermit crabs	3,20
Malacostraca	Decapoda	Brachyura	*Corystes*	Helmet crabs	2,50
Malacostraca	Decapoda	Brachyura	*Macropipus*	Macropipus	2,50
Malacostraca	Decapoda	Brachyura	*Macropodia rostrata*	Long-legged spider crab	2,50
Malacostraca	Decapoda	Brachyura	*Portunidae*	Swimming crabs	2,50
Malacostraca	Decapoda	Carcinidae	*Cancer pagurus*	Edible crab	2,50
Malacostraca	Decapoda	Carcinidae	*Carcinus maenas*	Shore crab	2,50
Malacostraca	Decapoda	Corophiidae	*Corophium* sp	Corophium sp	2,60
Malacostraca	Decapoda	Corophiidae	*Corophium volutator*	Mud shrimp	2,60
Malacostraca	Decapoda	Crangonidae	*Caprella linearis*	Skeleton shrimp	2,60
Malacostraca	Decapoda	Crangonidae	*Crangon allmanni*	Crangon allmanni	2,60
Malacostraca	Decapoda	Crangonidae	*Crangon crangon*	Brown shrimp	2,60
Malacostraca	Decapoda	Crangonidae	*Gastrosaccus spinifer*	Gastrosaccus spinifer	2,20
Malacostraca	Decapoda	Crangonidae	*Mysidae*	Mysidae	2,20
Malacostraca	Decapoda	Crangonidae	*Palaemon serratus*	Aesop prawn	2,60
Malacostraca	Decapoda	Crangonidae	*Pontophilus bispinosus*	Philocheras bispinosus bispinosus	2,60
Malacostraca	Decapoda	Crangonidae	*Pontophilus trispinosus*	Philocheras trispinosus	2,60
Malacostraca	Decapoda	Crangonidae	*Praunus flexuosus*	Chameleon shrimp	2,20
Malacostraca	Decapoda	Crangonidae	*Processa*	Processa	2,60
Malacostraca	Decapoda	Crangonidae	*Processa canaliculata*	Processa canaliculata	2,60
Malacostraca	Decapoda	Cumacea	*Cumacea*	Hooded shrimp	2,60
Malacostraca	Decapoda	Nephropidae	*Homarus gammarus*	European lobster	3,20
Malacostraca	Decapoda	Palaemonidae	*Palaemon elegans*	Grass prawn	2,60
Malacostraca	Decapoda	Polybiidae	*Macropipus holsatus*	Swimming crab	2,50
Malacostraca	Isopoda	Isopoda	*Idotea* sp	Idotea sp	2,30
Mollusca	Mollusca	Mollusca	*Mollusca*	Mollusca	2,60
Nematoda	Nematoda	Nematoda	*Nematoda*	Nematodes	2,10
Ophiuroidea	Ophiurida	Ophiuroidea	*Ophiura ophiura*	Serpent star	2,00
Ophiuroidea	Spatangoida	Loveniidae	*Echinocardium cordatum*	Sea-potato	2,00
Pisces	Pisces	Pisces	*Pisces*		3,60
Pisces	Atheriniformes	Aterinidae	*Atherina presbyter*	Sand-smelt	3,70
Pisces	Clupeiformes	Clupeidae	*Alosa fallax*	Twaite shad	2,92
Pisces	Clupeiformes	Clupeidae	*Clupea harengus*	Herring	3,40
Pisces	Clupeiformes	Clupeidae	*Sprattus sprattus*	Sprat	3,09
Pisces	Cyprinodontiformes	Belonidae	*Belone belone*	Garfish	3,68
Pisces	Gadiformes	Gadidae	*Ciliata mustela*	Five-bearded rockling	3,53
Pisces	Gadiformes	Gadidae	*Merlangius merlangus*	Whiting	3,83
Pisces	Gasterosteiformes	Gasterosteidae	*Gasterosteus aculeatus*	Stickleback	3,30
Pisces	Mugiliformes	Mugilidae	*Liza aurata*	Golden grey mullet	2,05
Pisces	Perciformes	Moronidae	*Dicentrarchus labrax*	Bass	3,60
Pisces	Perciformes	Ammodytidae	*Ammodytes tobianus*	Sandeel	4,15
Pisces	Perciformes	Ammodytidae	*Hyperoplus lanceolatus*	Greater sandeel	4,00

(*continued on next page*)

Table 1 (*continued*)

Class	Order	Family	Scientific name	Common name	Trophic position (–)
Pisces	Perciformes	Trachinidae	*Echiichthys vipera*	Lesser weever	4,40
Pisces	Perciformes	Callionymidae	*Callionymus lyra*	Dragonet	4,41
Pisces	Perciformes	Gobiidae	*Gobius niger*	Black goby	3,30
Pisces	Perciformes	Gobiidae	*Pomatoschistus minutus*	Sand goby	3,20
Pisces	Petromyzontiformes	Petromyzontidae	*Petromyzon marinus*	Lamprey	3,11
Pisces	Pleuronectiformes	Pleuronectidae	*Limanda limanda*	Dab	3,40
Pisces	Pleuronectiformes	Pleuronectidae	*Platichthys flesus*	Flounder	3,26
Pisces	Pleuronectiformes	Pleuronectidae	*Pleuronectes platessa*	Plaice	3,29
Pisces	Pleuronectiformes	Pleuronectidae	*Reinhardtius hippoglossoides*	Greenland halibut	4,60
Pisces	Pleuronectiformes	Solidae	*Buglossidium luteum*	Solenette	3,25
Pisces	Pleuronectiformes	Solidae	*Solea solea*	Sole	3,20
Pisces	Salmoniformes	Osmeridae	*Osmerus eperlanus*	Smelt	3,31
Pisces	Scorpaeniformes	Cottidae	*Myoxocephalus scorpius*	Bull-rout	3,90
Pisces	Scorpaeniformes	Cottidae	*Myoxocephalus quadricornis*	Four-horn sculpin	3,60
Pisces	Scorpaeniformes	Liparidae	*Liparis liparis*	Sea-snail	3,89
Pisces	Scorpaeniformes	Gobiidae	*Pomatoschistus lozanoi*	Lozano's goby	3,30
Pisces	Scorpaeniformes	Gobiidae	*Pomatoschistus microps*	Common goby	4,45
Pisces	Scorpaeniformes	Gobiidae	*Pomatoschistus* sp	Pomatoschistus sp	4,45
Pisces	Zeiformes	Zeidae	*Zeus faber*	Dory	4,50
Polychaeta	Annelida	Annelida	*Annelida*	Annelida	2,10
Polychaeta	Arenicolidae	Arenicolidae	*Arenicolidae*	Arenicolidae	2,10
Polychaeta	Phyllodocida	Aphrodita	*Aphrodita*	Sea mouse	2,10
Polychaeta	Phyllodocida	Nereididae	*Alitta virens*	Sandworm	2,10
Polychaeta	Phyllodocida	Nereididae	*Nereididae*	Nereididae	2,10
Polychaeta	Phyllodocida	Nereididae	*Nereis*	Nereis	2,10
Polychaeta	Phyllodocida	Opheliidae	*Ophelia limacina*	Ophelia limacina	2,10
Polychaeta	Phyllodocida	Phyllodocidae	*Arenicola marina*	Lugworm	2,10
Polychaeta	Phyllodocida	Phyllodocidae	*Lanice conchilega*	Sand mason worm	2,10
Polychaeta	Phyllodocida	Phyllodocidae	*Marenzelleria viridis*	Marenzelleria viridis	2,10
Polychaeta	Phyllodocida	Phyllodocidae	*Nephtys hombergii*	Catworm	2,10
Polychaeta	Phyllodocida	Phyllodocidae	*Phyllodoce maculata*	Phyllodoce maculata	2,10
Polychaeta	Phyllodocida	Phyllodocidae	*Scoloplos armiger*	Scoloplos armiger	2,10
Polychaeta	Polychaeta	Polychaeta	*Polychaeta*	Bristle worms	2,10
Polychaeta	Terebellida	Pectinariidae	*Lagis koreni*	Trumpet worm	2,10

$$PO_i \text{ or } TP_i = \alpha + f(Year) + \varepsilon_i \quad \varepsilon_i \sim N(0, \sigma^2) \qquad [2]$$

The model was cross-validated with different degrees of smoothing (SPAN) to determine the optimal SPAN based on the minimum residual sum of the root mean square error (RMSE). The evaluation of the GAM results was done following Swartzman et al. (1992) and MacKenzie and Schiedek (2007): The trend of the GAM model was drawn with 95% confidence limits. If a horizontal line could be drawn between the 95% confidence area of the fitted trend, the results of the GAM model was judged as no changes over time ($P > 0.05$).

In addition, the whole fish data set (including all species) was analysed, whereby the present range of trophic position *(TP*) of the various species (2010–2019) as described by Poiesz et al. (2020) was taken as reference. For all years and all species, the estimates of *TP* were compared with the reference period and scored as (1) above, (2) within or (3) below the 2010–2019 range. Next, trends in these scores over time were analysed per 5 year period.

All computations and analyses were done in R (R Core Team, 2021). The graphics were made using the ggplot package (Wickham, 2009).

3. Results

3.1. Fish data

The NIOZ archive contained information about 7031 stomachs of 43 fish species over the years 1932–1979. Data for the years 1980–2019 included information about another 5217 stomachs of 60 fish species, in total information about 12248 stomachs of 64 fish species. Records were not evenly distributed but clustered both with respect to years as well as fish species. Also, records of some species were only present in the 1940–1960's (skates and shark species), records of bass *Dicentrarchus labrax* (bass) only appeared in the samples in recent times and for some species only few records were available (see Supplementary materials Table S1). The archive data cluster around a few intervals: period 1947–1951; period 1962–1969; period 1975–1981; period 2005–2009 and the reference period 2010–2019 (Fig. 2A).

In total 117 different prey items were described over the years (Table 1). For detailed information see Supplementary materials Table S2. Number of species identified did not show a trend for the various Classes except for slightly higher number Pisces and Polychaetes in recent years (Fig. 2B,C,D,E).

For the analysis, fish species from the various functional groups and guilds were selected (Table 2). Trends with GAM in stomach content could be analysed for 15 species and trends in trophic position could be determined in 16 species.

3.2. Stomach content

3.2.1. All data

Within the reference period (2010–2019), Malacostraca were the most important Class of prey in the stomachs of the analysed Wadden Sea fish species based on the mean relative occurrence, followed by Pisces, Polychaetes and Bivalves (Fig. 3). The various periods each showed a larger interannual variability of prey mean relative occurrence than the reference period. During the period 2005–2009, the relative mean occurrence of the various prey classes was within the range of the reference period. In the period 1975–1981, more Polychaetes and more Bivalves were found as prey. During the period 1962–1969, also more Polychaetes were found as prey but less Pisces. The period 1947–1951 displayed a large variability: some years had more Pisces while other years had hardly any Pisces but more Malacostraca as prey (Fig. 3).

The Malacostraca prey (3706 records) mainly consisted of the family Crangonidae (2156 records, brown shrimps and other shrimps) and furthermore Copepods (415 records). Pisces (2601 records) were partly unidentified species (772 records) and furthermore Clupidae (394 records, mainly herring) and Gobiidae (339 records, mainly sand goby). In addition there were 533 records of Callionymidae prey, however this

Table 2

Overview of selected fish species from the NIOZ Archive, together with functional group and guild. (Near)-resident: Near-resident or resident species; JMM: juveniel marine migrants; MSV: Marine seasonal visitor. For each species, total number of stomachs and number of years with observations, split up into unpublished data (1932–2009) and reference data (2010–2019 after Poiesz et al., 2020), are listed. Type of analysis is indicated by X.

Scientific name	Common name	Functional group	Guild	Number of stomachs			Number of years with observations			Stomach content		Trophic position	
				Total	1932–2009	2010–2019	Total	1932–2009	2010–2019	Composition	GAM	Estimate	GAM
Belone belone	Garfish	Pelagic	(Near)-resident	32	10	22	16	8	8	x		x	
Clupea harengus	Herring	Pelagic	JMM	243	49	194	20	10	10	x	x	x	x
Sprattus sprattus	Sprat	Pelagic	JMM	51	20	31	15	7	8	x	x	x	x
Trachurus trachurus	Scad	Pelagic	MSV	109	29	80	20	10	10	x	x	x	x
Osmerus eperlanus	Smelt	Pelagic	MSV	120	14	106	15	7	8	x	x	x	x
Merlangius merlangus	Whiting	Benthopelagic	MSV	220	90	130	23	13	10	x	x	x	x
Trisopterus luscus	Bib	Benthopelagic	MSV	147	93	54	22	13	9	x	x	x	x
Gadus morhua	Cod	Benthopelagic	MSV	119	77	42	19	13	6	x	x	x	x
Anguilla anguilla	Eel	Benthopelagic	MSV	13	10	3	7	6	1	x		x	x
Ciliata mustela	Five-bearded rockling	Benthic	(Near)-resident	239	88	151	19	9	10	x	x	x	x
Platichthys flesus	Flounder	Benthic	(Near)-resident	456	182	274	28	18	10	x	x	x	x
Myoxocephalus scorpius	Bull-rout	Benthic	(Near)-resident	156	103	53	23	14	9	x	x	x	x
Zoarces viviparus	Viviparous blenny	Benthic	(Near)-resident	144	134	10	16	13	3	x	x	x	x
Pomatoschistus minutus	Sand goby	Benthic	(Near)-resident	133	97	36	14	7	7	x	x	x	x
Pleuronectes platessa	Plaice	Benthic	JMM	1048	942	106	33	24	9	x	x	x	x
Solea solea	Sole	Benthic	JMM	59	39	20	17	12	5	x	x	x	x
Limanda limanda	Dab	Benthic	MSV	1260	1224	36	29	21	8	x	x	x	x

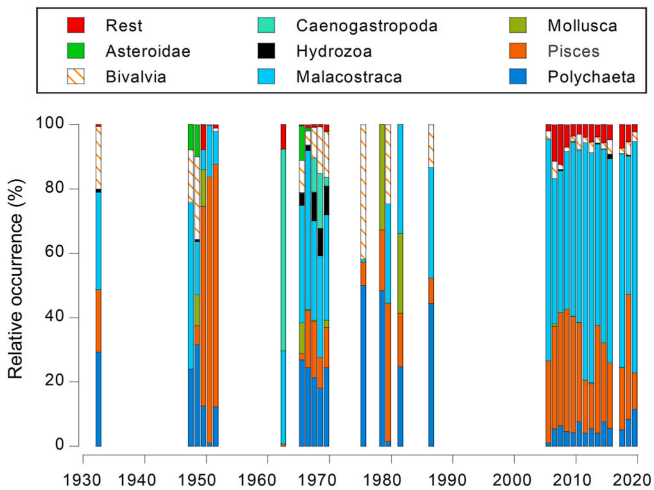

Fig. 3. Relative mean occurrence (%) of the most abundant prey classes in the stomachs of Wadden Sea fish species within the NIOZ archive (1932–2019). Only years with al least 50 observations are listed.

record is doubtful since it was based on a single observation of 512 prey items in one year (1949). The Polychaetes (2917 records) mainly referred to Annilida (2334 records) and furthermore Phyllodocidae (345 records, mainly *Lanice* spec. and *Nereis* spec.). The Bivalvia prey (1831 records) were mainly unidentified (949 records) and other Ensis spec. (829 records). For detailed information see Supplementary Material Table S2.

3.2.2. Individual species

The group of pelagic species (Fig. 4A) contained one (near)resident species (garfish *Belone belone*), two juvenile marine migrants (herring *Clupea harengus* and sprat *Sprattus sprattus*) and two marine seasonal visitors (scad *Trachurus trachurus* and smelt *Osmerus eperlanus*). Garfish mainly consumed Pisces (herring and to a lesser extent sandeel) but also regularly Malacostraca (mainly brown shrimp). Prey items for herring were mainly Malacostraca (mainly Copepods and to a lesser extent Gammarus, Corophium and Mysidae) and some Pisces (herring and sandeel), Polychaete, (mixture of species) and Bivalves (razor clams). Sprat mainly consumed Malacostraca (mainly consisting of Copepods and to a lesser extent shore crab and brown shrimp). For scad, main prey items were Malacostraca (mainly brown shrimp and shore and swimming crabs) and Pisces (mainly herring and sandeel). Malacostraca (mainly shrimps and swimming crabs and some Copepods) and Pisces (herring and various goby species) were also the main prey items of smelt.

The group of benthopelagic species (Fig. 4B) only contained four marine seasonal visitor species (whiting *Merlangius merlangus*, bib *Trisopterus luscus*, cod *Gadus morhua* and eel *Anguilla anguilla*). Whiting focused on Pisces (mainly herring, some sandeel and various goby species), Malacostraca (mainly shrimps, to a lesser extend crabs and some Mysis) and from 2000 on Autobranchia (*Ensis* spec.). Bib mainly consumed Malacostraca (shrimps, crabs and some Mydidae) and some Pisces (herring and to a lesser extend sand goby and sandeel). Main prey items for cod were Malacostraca (mainly brown shrimp and some shore crabs), some Pisces (mainly herring and some sandeel and goby species) and Polychaeta. Eel mainly preyed upon Polychaeta and Malacostraca (brown shrimps and shore crabs).

The group of demersal species (Fig. 4C) contained five (near)-resident species (five-bearded rockling *Ciliata mustela*, flounder *Platichthys flesus*, bull-rout *Myoxocephalus scorpius*, viviparous blenny *Zoarces viviparus* and sand goby *Pomatoschistus minutus*), two juvenile marine migrant species (plaice *Pleuronectes platessa* and sole *Solea solea*) and a marine seasonal visitor species (dab *Limanda limanda).* Five-bearded rockling focussed on Malacostraca (mainly brown shrimp but also crabs) and in recent years sometimes on Pisces (mainly herring and also goby species). Flounder consumed a variety of prey items but especially Polychaeta, Pisces (mainly herring and some goby species), Malacostraca (mainly brown shrimps and to a lesser extend *Corophium* and shore and swimming crabs) and some Bivalves. Bull-rout preyed mainly on Malacostraca (brown shrimp and shore and swimming crabs) and to a lesser extent on Pisces (mainly herring). Main prey items of viviparous blenny were Malacostraca (Amphipods, brown shrimp and some crabs) and some Polychaeta, Pisces (herring) and Bivalves. Sand goby preyed especially upon Malacostraca (Copepods, Amphipods, small shrimp and shore crabs) and also on some Polychaeta and Pisces (herring). Plaice consumed a variety of prey species, especially Polychaeta, Malacostraca (mainly shrimps and shore and swimming crabs and some Amphipods and Mysis), Bivalves and Caenogastropoda (Hydrobia). Sole focused on Polychaeta and Malacostraca (mainly shrimps and crabs and some Mysis). Dab consumed a variety of prey items with a focus on Polychaeta, Pisces (mainly herring and furthermore some sandeel), and Malacostraca (mainly brown shrimps and furthermore shore and swimming crabs).

For the group of pelagic species, for all prey items (except for one year for the occurrence of Malacostraca in the diet of herring) for which a GAM with 95% confidence limits could be calculated, a horizontal line could be drawn between the 95% confidence limits of the fitted trend, implying that the frequency of occurrence had not changed over time (Supplementary Material Fig. S1A and Table 3). For three benthopelagic species (whiting, bib and cod) a GAM with 95% confidence limits could be calculated for the Malacostraca and Pisces and in all cases a horizontal line could be drawn between the 95% confidence limits of the fitted trend, implying that the frequency of occurrence of Malacostraca and Pisces had not changed over time for whiting, bib and cod (Supplementary Material Fig. S1B and Table 3). For the group of demersal species, for all prey items (except for the occurrence of Bivalves in the diet of plaice) for which a GAM with 95% confidence limits could be calculated, a horizontal line could be drawn between the 95% confidence limits of the fitted trend, implying that the frequency of occurrence had not changed over time (Supplementary Material Fig. S1C and Table 3).

All GAM parameters of the various trends in prey occurrence of the various fish species [smoother span, number of observations, number of parameters, standard error, smoother matrix, effective degrees of freedom (edf) and the p-value] are presented in Supplementary Material Table S3.

3.3. Trophic position

For all individual years of the reference period 2010–2019, estimated trophic levels of the stomach contents based on a rerun with trophic values of identified prey Class were significantly related with original estimates based on trophic values of identified prey Species (Fig. 5).

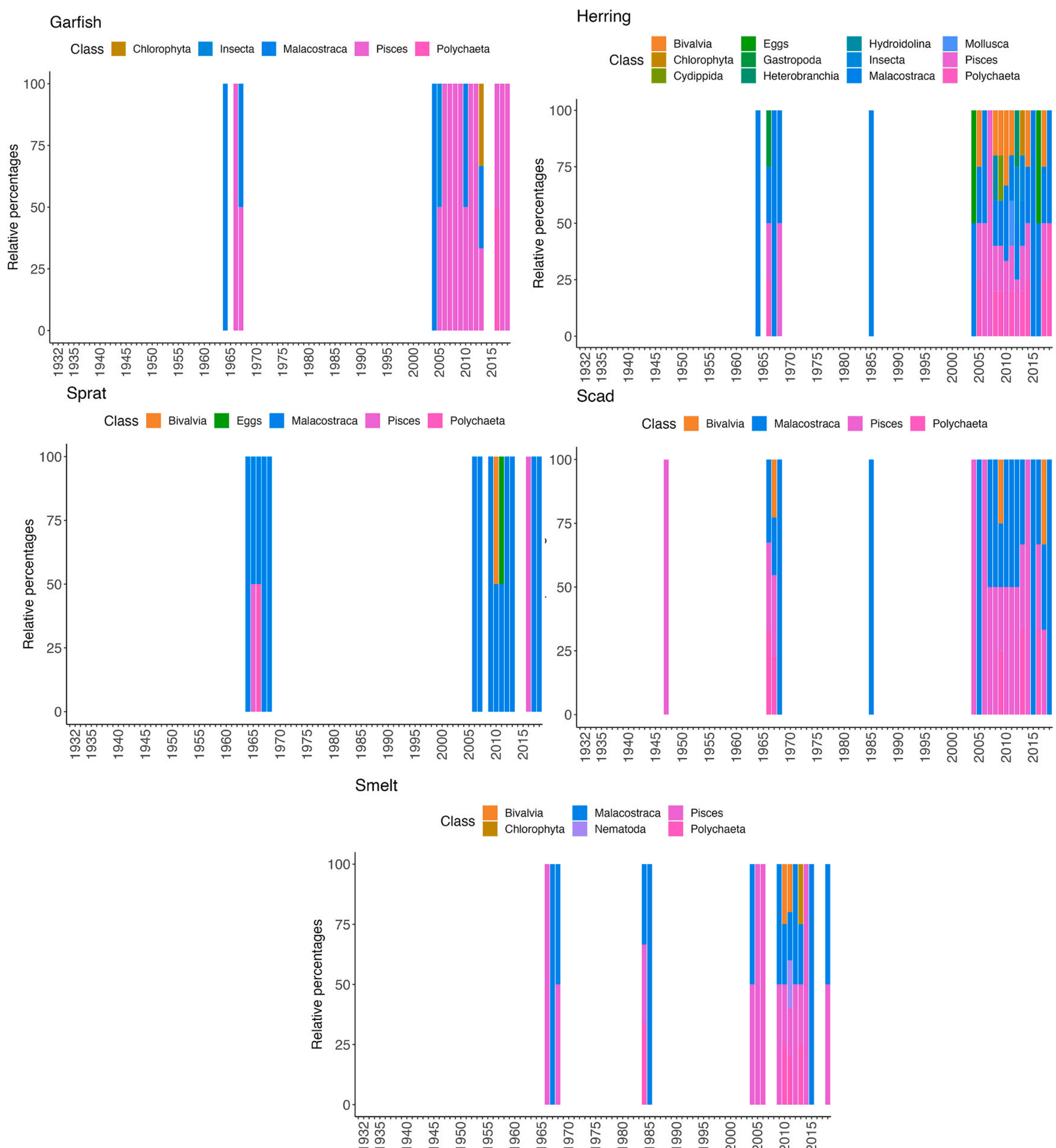

Fig. 4A. Mean occurrence of various prey items in the stomachs of the selected pelagic species; the (near)-resident species garfish *Belone belone*; the juvenile marine migrants herring *Clupea harengus* and sprat *Sprattus sprattus* and the marine seasonal visitors scad *Trachurus trachurus* and smelt *Osmerus eperlanus*.

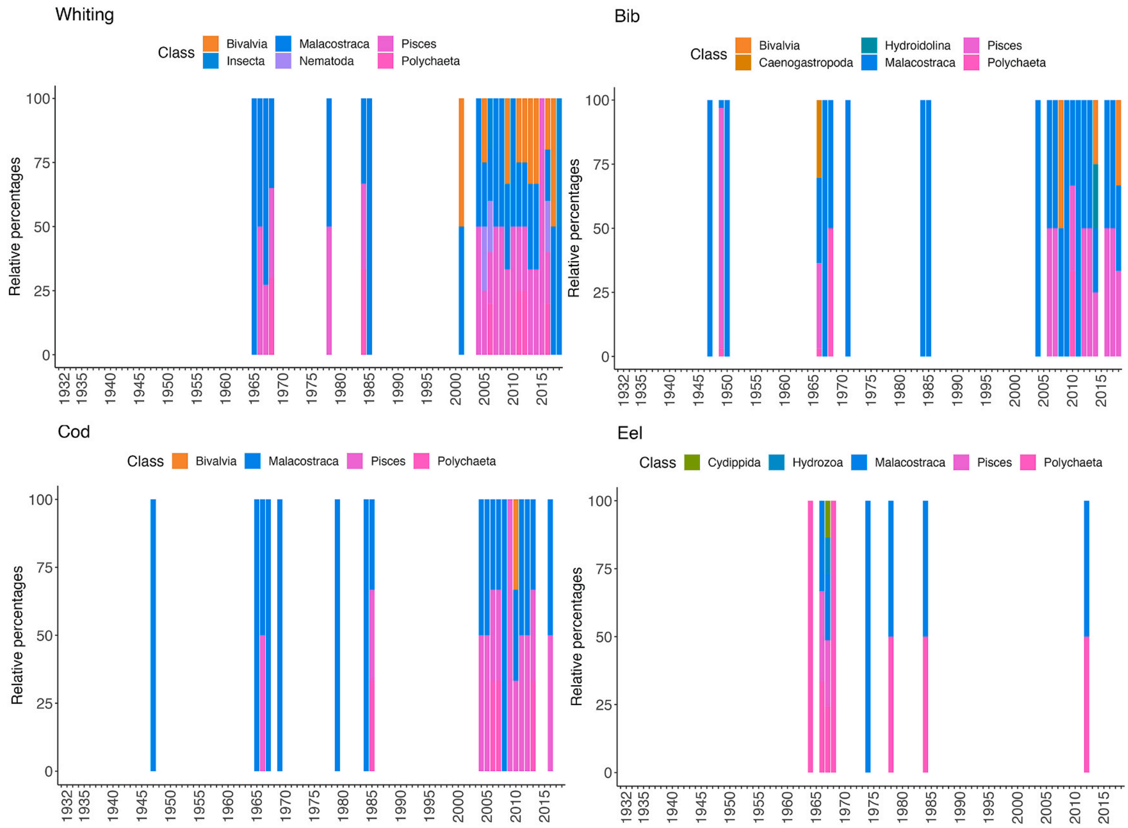

Fig. 4B. Mean occurrence of various prey items in the stomachs of the selected benthopelagic species; the marine seasonal visitor species (whiting *Merlangius merlangus*, bib *Trisopterus luscus*, cod *Gadus morhua* and eel *Anguilla Anguilla*.

3.3.1. *All data*

Variability in trophic position of the different prey species was low for most Classes, except for Malacostraca (23%) and Pisces (38%) (Table 1). For the reference period (2010–2019) in almost all fish species, the estimated trophic position showed variation over a range of ~2 units (Table 4).

The estimated mean trophic position *(TP)* of the various fish species over the years can be found in Supplementary Material Table S4. In the period 2005–2009, estimated mean trophic position were within those of the period 2010–2019 (Fig. 6). Between 1970 and 1990, the percentage of species with estimates of trophic position within the reference range was lower, around 50–60 % and a higher percentage of species had estimates below the reference range compared with above the range (Fig. 6). During the period 1945–1950 the percentage of species with estimates respectively below and above the reference range were almost similar (Fig. 6).

3.3.2. *Individual species*

In 16 species, enough data were present to apply General Additive Models (GAMs) to visualise and analyse trends over time (Fig. 7ABC).

In all pelagic (twaite shad, herring, sprat, scad and smelt), benthopelagic (whiting, bib, cod and eel) and demersal species (five-bearded rockling, flounder, bull-rout, viviparous blenny, sand goby, plaice, sole and dab), a horizontal line could be drawn between the 95% confidence limits of the fitted trend, implying no change over time (Fig. 7ABC). All GAM parameters of the various trends in trophic position of the various fish species [smoother span, number of observations, number of parameters, standard error, smoother matrix, effective degrees of freedom (edf) and the p-value] are presented in Supplementary Material Table S5.

4. Discussion

4.1. *Quality and limitations of the NIOZ archive data*

Long-term series are unique and in principle valuable data sets, however a precondition is that the quality and the limitations of the data can be judged and that potential pitfalls can be identified. Wiltshire and Dürselen (2004) carried out a quality control of the Helgoland Reede long-term phytoplankton data archive (1962 – present) and listed a number of typical general problems they came across. The most important issues that can be expected for all long-term series can be summarized as:

- lack of meta-information, especially from the past;
- the mismatch between the original records on paper and the electronical archive;
- outdated taxonomic nomenclature and synonyms;
- different procedures over time;
- different investigators over time with different taxonomic knowledge.

Also the NIOZ archive data suffers from some of these problems. The NIOZ archive also lacks meta-information with respect to information about potential digestion between time of catch and of stomach analysis. However, most of the records originate from NIOZ courses where fish were dissected immediately after being caught. Stomach content of rare fish species from fishermen might have suffered from digestion: often these stomachs were empty or could not be identified. The NIOZ archive did not suffer from a mismatch between the original records on paper and the electronical archive, because the data were never electronically archived in the past. The problem of outdated taxonomic nomenclature and synonyms occurred but was solved by using WoRMS (http://www.

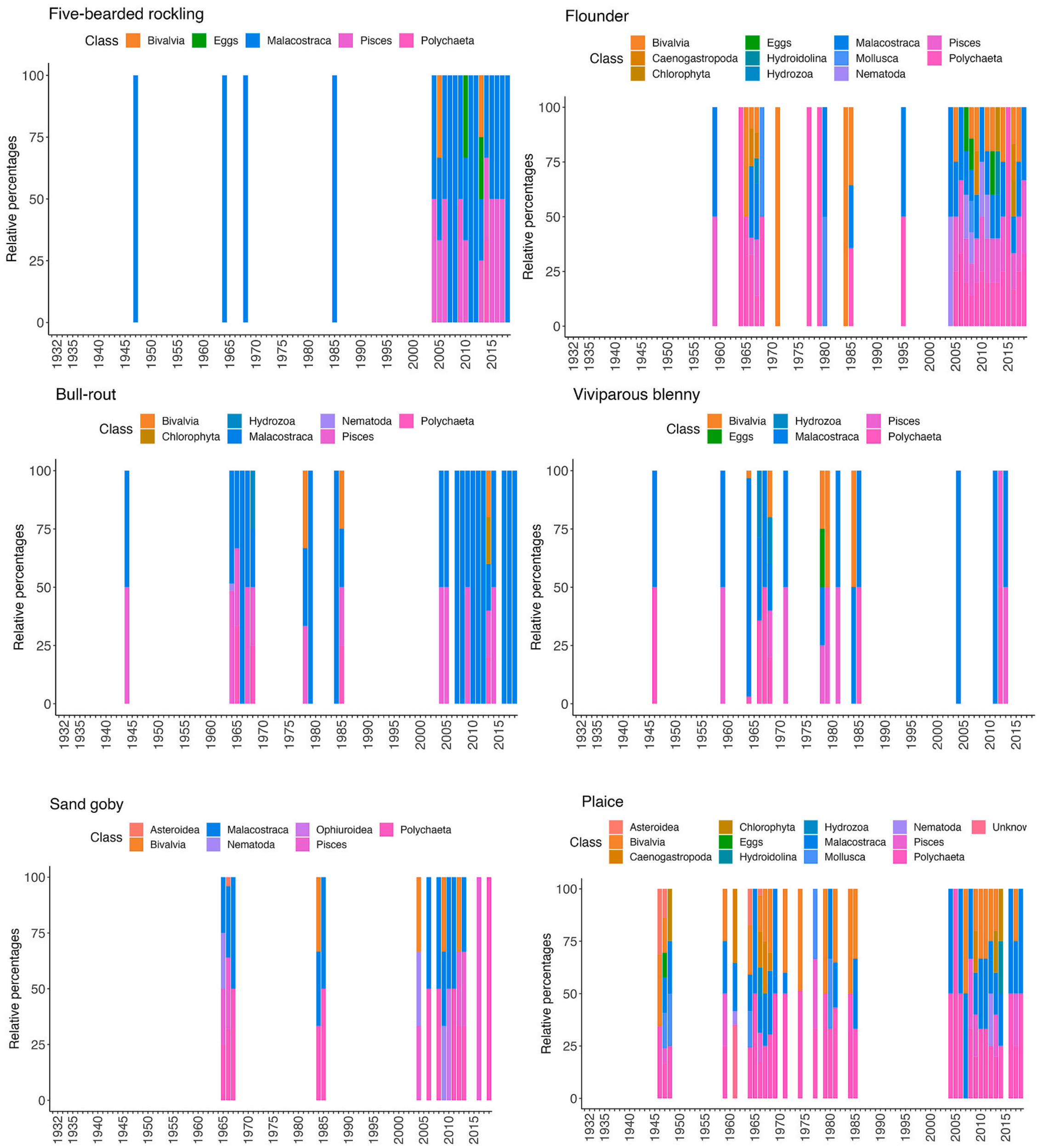

Fig. 4C. Mean occurrence of various prey items in the stomachs of the selected benthic species; the (near)-resident species five-bearded rockling *Ciliata mustela*, flounder *Platichthys flesus*, bull-rout *Myoxocephalus scorpius*, viviparous blenny *Zoarces viviparus* and sand goby *Pomatoschistus minutus*; the juvenile marine migrant species plaice *Pleuronectes platessa* and sole *Solea solea* and the marine seasonal visitor species dab *Limanda limanda*, thick-lipped grey mullet *Chelon labrosus* and lesser weever *Echiichthys vipera*.

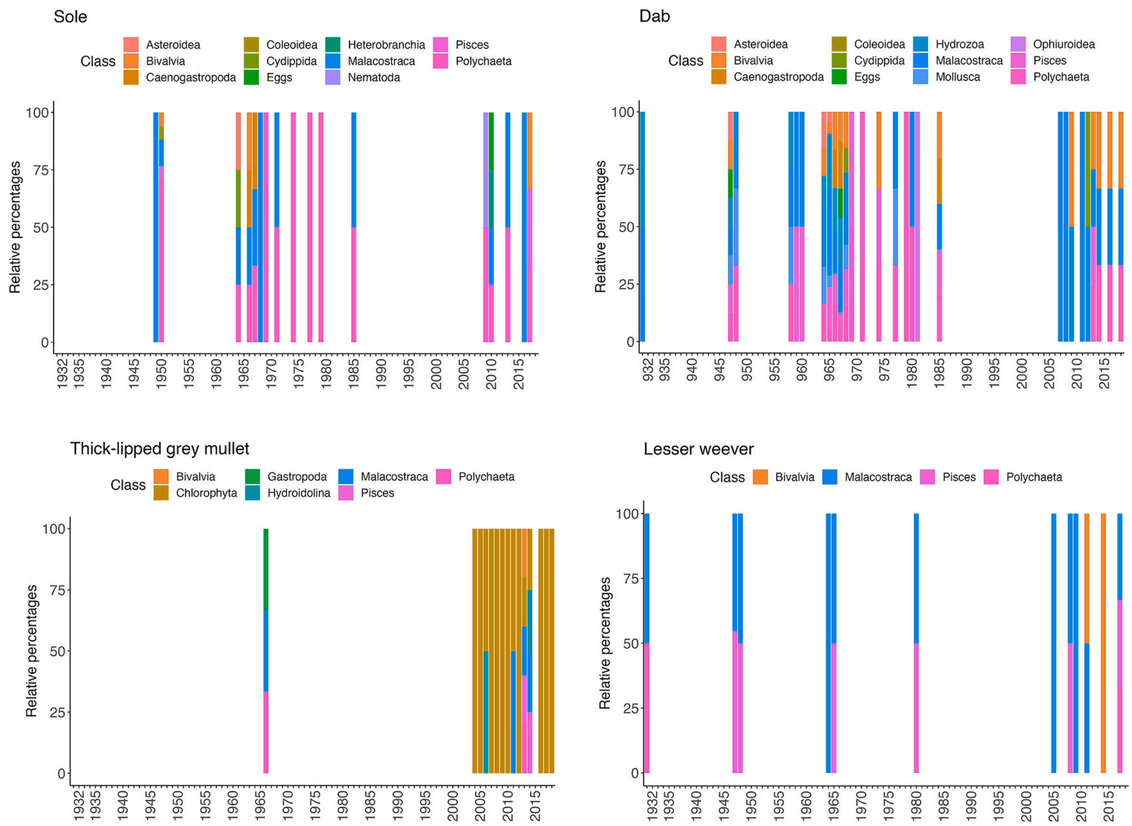

Fig. 4C. (*continued*).

marinespecies.org) for checking species, family, genus and class name of all fish and prey records. As far as we can check in the records, all analyses have always been supervised and/or carried out by qualified NIOZ staff with taxonomic knowledge.

Most striking are the differences in amount of data and in level of taxonomic identification of stomach content over time. From 1980 onwards, fish were collected regularly in spring and summer and until 1980 only randomly as part of NIOZ courses and landings from fishermen. This means that despite the more than 12.000 records of stomach content analysis for the fish community of the Wadden Sea, the dataset shows a large patchiness and variability both with respect to the years in which data were collected and in the fish species analysed. Surprisingly, level of taxonomic identification of prey over time hardly affected the estimate of the trophic position. A sensitivity analysis for the reference period 2010–2019 showed that estimated trophic levels based on prey Class were significantly related with original estimates based on prey Species.

By interpreting the results of the analysis of the NIOZ archive data, these restrictions should be kept in mind.

4.2. Wadden Sea baseline

What would be a realistic baseline for the Wadden Sea system and in particular for its fish fauna is open for debate. The Wadden Sea has been under the influence of anthropogenic stress for centuries (see for instance Lotze, 2005, 2007). Stress factors caused by human-induces activities (overfishing and pollution events), could theoretically be reduced or stopped. This, however, might be not pragmatic. However, other factors such as habitat loss are even more difficult to reverse. The last extensive habitat loss in the western Dutch Wadden Sea took place in the Marsdiep tidal basin in the western part in 1932 with the exclosure of the Zuiderzee estuary by the Afsluitdijk and in the eastern Dutch Wadden Sea in 1964 with the exclosure of the Lauwers (Wolff, 1983). This means that for the Marsdiep tidal basin a baseline before 1932 is unrealistic with respect to any analyses with more recent data, including the present situation. The low fishing pressure and low level of pollution (nutrients, chemicals) during the second world war would plea for a realistic baseline around 1945 for the Wadden Sea system.

Quantitative information about the Dutch Wadden Sea system for the period around 1945 is scarce except for water temperature and salinity data (van Aken, 2008a, 2008b) and remains fragmentary until the beginning of the 1970s, despite the start of nutrient measurements (phosphorus) from 1949 onwards (Postma, 1954) and primary production estimates (Postma and Rommets, 1970) and demersal fish surveys in 1963–1965 (Creutzberg and Fonds, 1971). Only for the last half century from the 1970's onwards more systematic information is available with presently time series about various abiotic and biotic ecosystem components such as water temperature and salinity, primary production, the benthic community, fish fauna, wading birds and marine mammals for various parts of the Wadden Sea. For an overview see the various quality status reports of the Wadden Sea (https://qsr.waddensea-worldheritage.org/).

The present study contains information on trophic structure based on stomach content dating back to the early 1930's. The Wadden Sea ecosystem in the 1930's will have been a system with lower nutrient concentrations (van der Veer et al., 1989; van Raaphorst and van der Veer, 1990; van Raaphorst and de Jonge, 2004) but nevertheless a system with a higher fish abundance compared to the present ecosystem. A higher fish abundance in the past is supported by the fact that, before and after the second world war, there was a profitable commercial fyke net fishing in the area. However catches and profitability decreased rapidly until the last fishing company was terminated in 1966 and taken over by NIOZ to start the long-term monitoring series (van der Veer et al., 2015).

Table 3
Changes over time in main prey groups (grey) of selected fish species from the NIOZ Archive 1931–2019. (Near)-resident: Near-resident or resident species; JMM: juveniel marine migrants; MSV: Marine seasonal visitor. Significance of the GAM trend is indicated (n.s.: not significantly deviating from horizontal line or P < 0.05). Only years with more than 5 observations are included.

Scientific name	Common name	Functional group	Guild	Algae	Bivalves	Malacostraca	Pisces	Polychaeta
Clupea harengus	Herring	Pelagic	JMM		n.s.	P < 0.05	n.s.	n.s.
Sprattus sprattus	Sprat	Pelagic	JMM			n.s.		
Trachurus trachurus	Scad	Pelagic	MSV			n.s.	n.s.	
Osmerus eperlanus	Smelt	Pelagic	MSV			n.s.	n.s.	
Merlangius merlangus	Whiting	Benthopelagic	MSV			n.s.	n.s.	
Trisopterus luscus	Bib	Benthopelagic	MSV			n.s.	n.s.	
Gadus morhua	Cod	Benthopelagic	MSV			n.s.	n.s.	
Ciliata mustela	Five-bearded rockling	Benthic	(Near)-resident			n.s.	n.s.	
Platichthys flesus	Flounder	Benthic	(Near)-resident		n.s.	n.s.		
Myoxocephalus scorpius	Bull-rout	Benthic	(Near)-resident			n.s.	n.s.	
Zoarces viviparus	Viviparous blenny	Benthic	(Near)-resident			n.s.		
Pomatoschistus minutus	Sand goby	Benthic	(Near)-resident			n.s.		n.s.
Pleuronectes platessa	Plaice	Benthic	JMM		P < 0.05	n.s.		n.s.
Solea solea	Sole	Benthic	JMM			n.s.		n.s.
Limanda limanda	Dab	Benthic	MSV			n.s.	n.s.	n.s.

The much and varying variability in the stomach content for any given species within the period 1930–2019 raises the question whether stomach content data of fish species is absent in particular years and decades because the fish species were absent or rare in the ecosystem, or because they were simply not targeted during that time. For most species, missing data indicate that they were not targeted: from the 1980's onwards, stomach content data were collected from a long-term monitoring programme of the fish fauna with a passive fish trap near the entrance of the Wadden Sea in spring and autumn and during that period no species went extinct and common species were caught almost every year (Poiesz et al., 2020). Only most of the skate and shark species disappeared from the Wadden Sea from the 1960's onwards, similar as in other areas (Walker and Heessen, 1996; Dulvy and Reynolds, 2002; Reynolds et al., 2005; Heessen et al., 2015; Bom et al., 2020; Poiesz et al., 2021b).

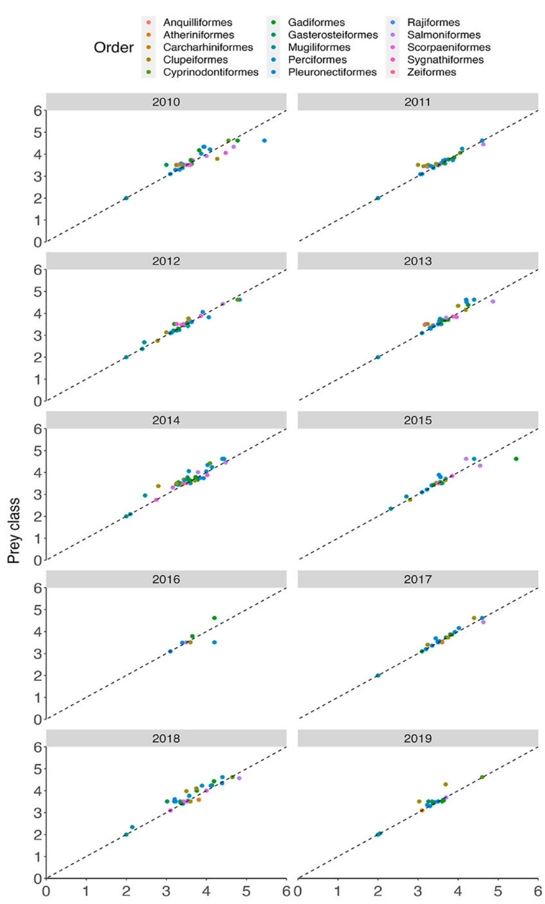

Fig. 5. Comparsion of estimated TP values of individual fish species per 5 year period with the range of TP of the reference period 2010–2019.

4.3. Prey consumption

A variety of sources are available for the reconstruction of the fish food web structure, ranging from anecdotal and semi-quantitative information about species composition (see for instance Roberts, 2007) to quantitative analysis of archaeological remains such as of bones and otoliths. The latter can include stable isotope analysis (Fry, 2006; Middelburg, 2014; Phillips et al., 2014; Tsutaya et al., 2021), genetics, age and growth analyses (see for example Bolle et al., 2004, Cuveliers et al., 2007) and stomach content analysis [such as deriving trophic structure and predator−prey interactions (Hynes, 1950; Baker et al., 2014)]. Stomach content analysis provides information about recently ingested prey items only, while especially regurgitation and digestion are factors that may cause prey items to be missed or overlooked. The extended period of sampling may have partly overcome these limitations, however, for rare species an insufficient number of stomachs may have been sampled to cover all possible prey species (Karachle and Stergiou, 2017; Mulas et al., 2015).

Recent studies in two different parts of the Wadden Sea reveal that, although most of the Wadden Sea fish species are rather omnivorous, their food requirements are fuelled by a few key prey species (Kellnreiter et al., 2012; Poiesz et al., 2020). This omnivorous feeding behaviour can also be recognized in the stomach content compositions of the Wadden Sea fish fauna over the last half century. Interannual variations in stomach composition do occur due to variations in the level of detail of the stomach content analysis over the years as well as variations in prey abundance. Nevertheless, a few groups, Bivalvia/Autobranchia, Polychaeta, Malacostraca (mainly Decapoda: shrimps and crabs) and Pisces, were the main prey items from the 1930's onwards to recent decades. A few key species as main pathways of energy flow to higher trophic levels might be a general characteristic for estuarine systems; it has been described for other areas also, such as Amphipods and Copepods in the French Chanche estuary (Selleslagh et al., 2012).

Trends in prey occurrence in the stomachs could be determined for some prey items in some individual fish species. However, the analysis

Table 4
Size frequency distribution of estimated trophic position (TP) of individual fish for the period 2010–2019.

Scientific name	Common name	Trophic position (TP)									
		1.00–1.49	1.50–1.99	2.00–2.49	2.50–2.99	3.00–3.49	3.50–3.99	4.00–4.49	4.50–4.99	5.00–5.49	Total
Agonus cataphractus	Hooknose				1		28	1	2		32
Alosa fallax	Twaite shad					7	138	23	33		201
Ammodytes tobianus	Sandeel					3	6				9
Anguilla anguilla	Eel					1	8				9
Aphia minuta	Transparent goby										
Arnoglossus laterna	Scaldfish						24	1			25
Aspitrigla cuculus	Red gurnard										
Atherina presbyter	Sand-smelt			1	1	6	30	2	2		42
Belone belone	Garfish					2	2	1	26		31
Callionymus lyra	Dragonet						1		1		2
Callionymus reticulatus	Reticulated dragonet					1					1
Chelon auratus	Golden grey mullet	1		88	1	4	5				99
Chelon labrosus	Thick-lipped grey mullet			55	2	2	16	2	5		82
Chelon ramada	Thin-lipped grey mullet			3							3
Ciliata mustela	Five-bearded rockling				3	3	390	17	25		438
Clupea harengus	Herring			8	1	26	220	12	33		300
Cyclopterus lumpus	Lumpsucker				1		26	2			29
Dicentrarchus labrax	Bass			3	1	52	446	33	100		635
Dipturus batis	Skate										
Echiichthys vipera	Lesser weever					2	3	1			6
Engraulis encrasicolus	Anchovy						2				2
Eutrigla gurnardus	Grey gurnard						1				1
Gadus morhua	Cod					1	67	10	10		88
Gasterosteus aculeatus	Stickleback			2	1	11	58		2	1	75
Gobius niger	Black goby										
Hyperoplus lanceolatus	Greater sandeel						1		9		10
Limanda limanda	Dab					11	27	1	3		42
Liparis liparis	Sea-snail						86	2	0		88
Lipophrys pholis	Shanny								1		1
Melanogrammus aeglefinus	Haddock										
Merlangius merlangus	Whiting				1	19	170	24	25		239
Microstomus kitt	Lemon sole					1					1
Mustelus mustelus	Smooth hound										
Myoxocephalus scorpius	Bull-rout				1	2	100	12	3		118
Neogobius melanostomus	Round goby						7		1		8
Osmerus eperlanus	Smelt			1		11	110	13	33		168
Pholis gunnellus	Butterfish					2	5				7
Phrynorhombus norvegicus	Norwegian topknot										
Platichthys flesus	Flounder			2	2	114	276	14	49		457
Pleuronectes platessa	Plaice			1	2	66	39	3	10		121
Pollachius pollachius	Pollack						46	13	7		66
Pollachius virens	Saithe				1	2	6	7	8		24
Pomatoschistus lozanoi	Lozano's goby					1	10				11
Pomatoschistus microps	Common goby					1	4				5
Pomatoschistus minutus	Sand goby					14	22		4		40
Salmo salar	Salmon										
Salmo trutta	Sea trout					3	47	8	236		294
Sardina pilchardus	Pilchard			4			14		3		21
Scomber scombrus	Mackerel						5	6	8		19
Scophthalmus maximus	Turbot				1	2	58	11	19		91
Scophthalmus rhombus	Brill						13	1	10		24
Solea solea	Sole				1	16	6		5		28
Sparus aurata	Gilt-head sea bream						2				2
Sprattus sprattus	Sprat			1		1	37		3		42
Squalus acanthias	Spurdog										
Syngnathus acus	Greater pipefish						18	2	2		22
Syngnathus rostellatus	Nilsson's pipefish						33				33
Taurulus bubalis	Sea scorpion					1	21				22

(*continued on next page*)

Table 4 (*continued*)

Scientific name	Common name	Trophic position (TP)									
		1.00–1.49	1.50–1.99	2.00–2.49	2.50–2.99	3.00–3.49	3.50–3.99	4.00–4.49	4.50–4.99	5.00–5.49	Total
Trachinus draco	Greater weever										
Trachurus trachurus	Scad					4	35	12	79		130
Trigla lucerna	Tub gurnard				1		19	2			22
Trisopterus luscus	Bib					3	106	2	6		117
Trisopterus minutus	Poor cod					1	3				4
Zeus faber	Dory										
Zoarces viviparus	Viviparous blenny			1		3	4	1	2		11

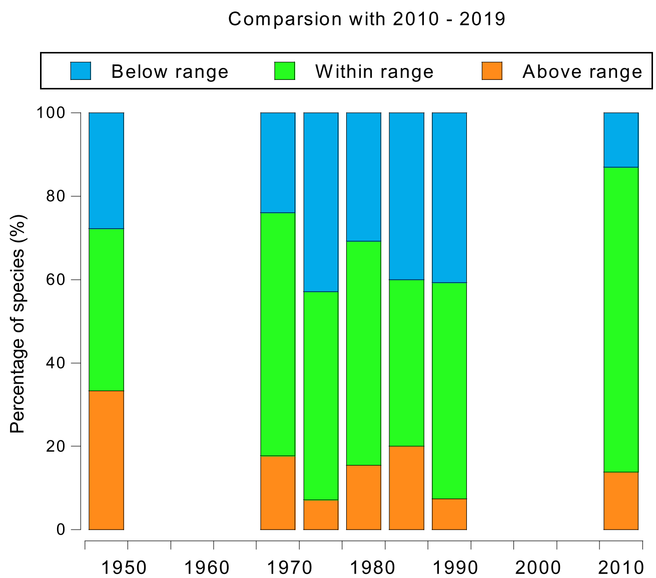

Fig. 6. Comparison of estimated mean TP values of all fish species per 5-year period to the reference period TP range (2010–2019). For more information see text.

was hampered by large patchiness and variability in the data and in the variability in the level of detail of the stomach content analysis. In all fish species that could be analysed, prey occurrence showed fluctuations over time. The most important prey species of the Malacostraca, the brown shrimp and the shore crab, both showed large interannual fluctuations in the Dutch Wadden Sea, with a general increase in both species over a 40 yr period (Tulp et al., 2012). Similar fluctuations were observed in secondary production of intertidal bivalves and polychaetes, however without a clear trend over time (Beukema and Dekker, 2022). Also the Wadden Sea fish community showed strong interannual fluctuations in abundance, added to a clear decline from the 1980s until the early 2000s (Tulp et al., 2008; van der Veer et al., 2015). Herring, the most important fish prey species, showed strong variation among years and fluctuated in abundance within one order of magnitude (van der Veer et al., 2015). Therefore, the fluctuations in stomach content composition partly reflects interannual variability in absolute and relative abundance of the most important prey groups.

The large patchiness and variability in the data resulted in large confidence intervals of the GAM smoother over time. Despite the large fluctuations in prey occurrence in the stomachs of the various fish species, hardly any significant differences between years were found (except for the occurrence of Pisces in the diet of smelt and sand-smelt and the occurrence of Malacostraca in the diet of sole and dab). Furthermore, no trends in prey occurrence over time were found in the various species analysed. This means that amphipod crustaceans, brown shrimps and crabs, juvenile herring and gobies and to a lesser extend bivalves and polychaetes are not only the key prey species presently (Poiesz et al., 2020) but already had a pivotal position in the fish food web in the past, at least from the 1930's onwards (this study).

4.4. Trophic position

The large patchiness in the data for all Wadden Sea fish species with respect to years of sampling, results in a mozaik of snapshots of trophic positions of individual species over time and in a number of species with enough data to apply General additive models (GAMs) to visualise and analyse trends over time. The analysis of the complete data set and the analyses of the individual species both indicated that trophic positions during the period 1930–2010 were variable but did not significantly differ from those in the present reference period (as described in Poiesz et al., 2020). The variability in individual stomach contents, and hence in the estimates of trophic position, illustrates the omnivorous character of most of the fish species in the Wadden Sea: current day estimations of trophic position varies by 2 units for most fish species (Poiesz et al., 2020, Table 3). It cannot be excluded that the present dataset with high sampling variability might be not robust enough to identify trends over time for these fish species with an inherent large individual variability in trophic position.

On the other hand, network analyses indicate that estuaries are rather stable systems, where a few species such as for instance clupeids, flatfish and gobies are able to cope with the inherent cyclical and seasonal perturbations: those species are robust and are responsible for a stable system (Lobry et al., 2008). In the western Dutch Wadden Sea there are also no trend indications in the number of species caught over the period 1960–2010 (van der Veer et al., 2015). The fact that in this study no trend in trophic position was found in species belonging to different modes of life (pelagic, benthopelagic and demersal) and guild (near-resident, juvenile marine migrant or seasonal visitor) might imply that this could also hold true for the other species not analysed in this study.

Although estuaries might be rather stable systems, serious impacts of anthropogenic stress have nevertheless been documented for many of these systems (see for instance Kennish, 1991, 2002; Chapman and Wang, 2001), including the Wadden Sea (Lotze, 2005, 2007). With respect to the fish fauna, this has led to the disappearance of most skate and shark species in the area, causing a loss of biodiversity in the Wadden Sea from the 1960's onwards, similar to those reported in other areas (Walker and Heessen, 1996; Dulvy and Reynolds, 2002; Reynolds et al., 2005; Heessen et al., 2015; Bom et al., 2020; Poiesz et al., 2021b). Before the 1960s, the Wadden Sea fish community did include skate and sharks, top predators with a relatively high trophic position.

The present study does not indicate any changes in trophic position of individual species in the western Dutch Wadden Sea over the last 80 years. This may be different at the community level. Although fish species composition in the western Wadden Sea has shown to be rather robust, species composition does show some interannual variation (van der Veer et al., 2015). Some species have also disappeared in the past,

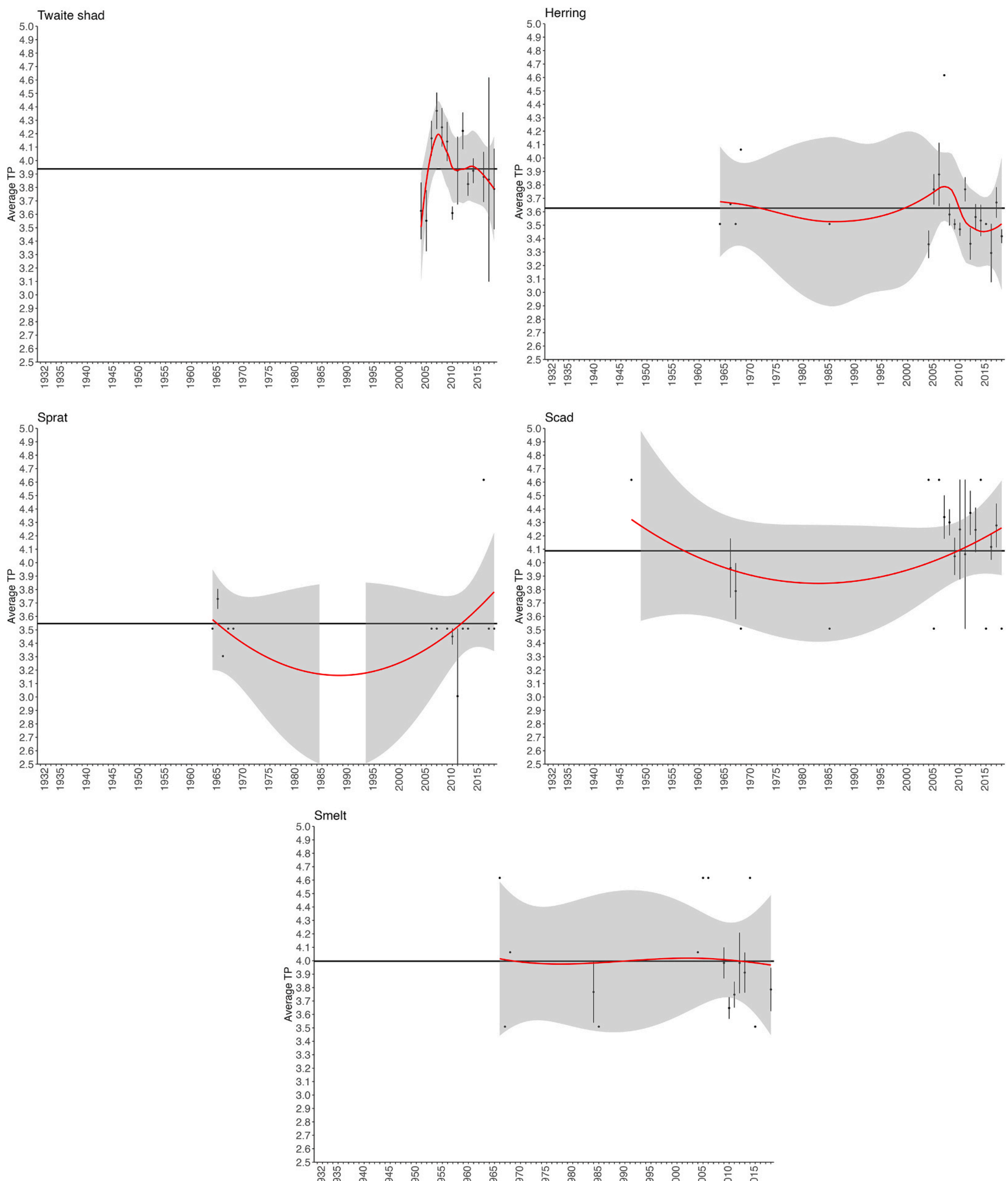

Fig. 7A. Mean trophic position (−) of the selected pelagic species; the (near)resident species twaite shad *Alosa fallax*; the juvenile marine migrants herring *Clupea harengus* and sprat *Sprattus sprattus* and the marine seasonal visitors scad *Trachurus trachurus* and smelt Osmerus eperlanus.

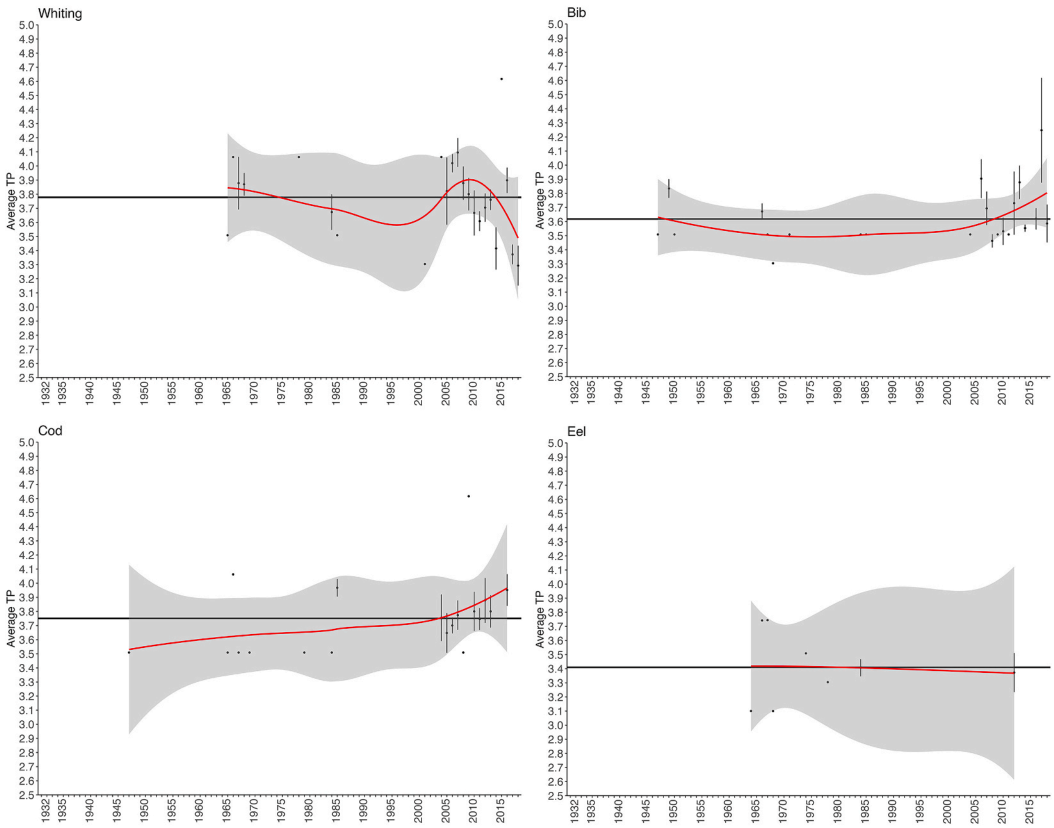

Fig. 7B. Mean TP (—) of the selected benthopelagic species; the marine seasonal visitor species whiting *Merlangius merlangus*, bib *Trisopterus luscus*, cod *Gadus morhua* and eel *Anguilla Anguilla.*

such as most of the skate and shark species. Furthermore, year-to year fluctuations in the relative abundance of the various fish species (Tulp et al., 2008; van der Veer et al., 2015) will be reflected in interannual variations in the trophic structure of the fish community. In the western Wadden Sea, the trophic structure of this community showed indeed some fluctuations from 1980 to 2011. For both the demersal and benthopelagic fish fauna the trophic position remained the same, while for pelagic fish the mean fell from about 3.9 to 3.1., mainly due to the decrease in abundance of predatory pelagic fish such as cod and garfish (van der Veer et al., 2015).

The 10-fold decrease in total biomass of the catches of both pelagic and demersal species from 1980 to 2011 (van der Veer et al., 2015) illustrates the degradation of the trophic role of the fish community at the ecosystem level in the western Wadden Sea. To what extent this has affected ecosystem functioning is unclear. In the North Sea, the depletion of demersal fish species in the period 1973–2000 appears to have released the benthos from "top-down" biomass control, leading to an increase in benthic production and invertebrates (Heath, 2005). To what extent the trophic structure of the fish community in the western Wadden Sea are a reflection of a more general pattern also in the other tidal basins of the Wadden Sea is unclear. The fact that most species are omnivorous and species composition appears to be largely the same at a large scale (Kühl and Kuipers, 1983; Kellnreiter et al., 2012; Meyer et al., 2016; Poiesz et al., 2020) might suggest a general pattern in trophic position of the fish species in the Wadden Sea. However, the fact that local and interannual differences were found in the abundance of demersal fish in the western, central and eastern part of the Wadden Sea and in its coastal regions (Tulp et al., 2017) implies that at the community and ecosystem level the trophic structure of the fish community may differ to some extent.

4.5. Conclusive remarks

In this study, trends in prey species consumed and in trophic position were analysed and by means of stomach content information compared to the present situation (2010–2019) for 18 omnivorous fish species in the western Dutch Wadden Sea. Prey consumption of different fish species showed variability over time, but without a change over time. Also, in all 18 species, no significant change in mean trophic position over time could be found. Despite the general decrease in fish abundance in the area (van der Veer et al., 2015). The present study does not indicate any changes in trophic position of individual species in the western Dutch Wadden Sea over the last 80 years despite the serious level of anthropogenic stress (pollution, eutrophication events, climate change) and the decrease in fish abundance in the area.

CRediT authorship contribution statement

Suzanne S.H. Poiesz: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Project administration, Formal analysis, Data curation, Conceptualization. **Johannes IJ. Witte:** Methodology. **Henk W. van der Veer:** Writing – review & editing, Writing – original draft, Validation, Supervision.

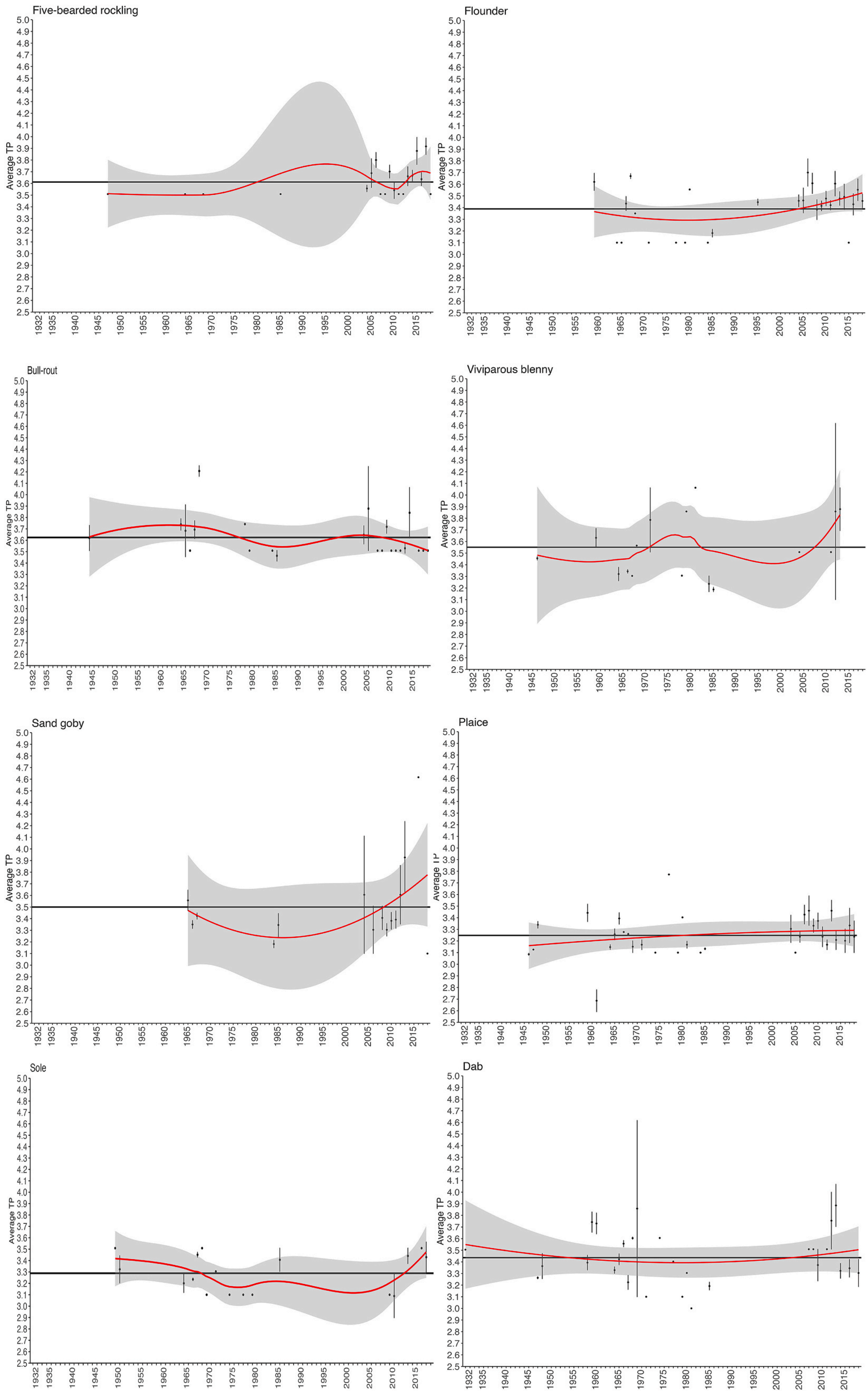

Fig. 7C. Mean TP (–) of the selected benthic species; the (near)-resident species five-bearded rockling *Ciliata mustela*, flounder *Platichthys flesus,* bull-rout *Myoxocephalus scorpius*, viviparous blenny *Zoarces viviparus* and sand goby *Pomatoschistus minutus*; the juvenile marine migrant species plaice *Pleuronectes platessa* and sole *Solea solea* and the marine seasonal visitor species dab *Limanda limanda*.

Declaration of competing interest

The authors declare that they have no competing interests.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2024.108912.

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