Historical trophic ecology of some divergent shark and skate species in the Dutch coastal North Sea zone

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Abstract

Over the last century the fish community of the Dutch coastal North Sea zone has lost most its shark and skate species. Whether their disappearance has changed the trophic structure of these shallow waters has not been properly investigated. In this study historical dietary data of sharks and skates, being in the past (near)-residents, juvenile marine migrants and marine seasonal visitors of the Dutch coastal North Sea zone were analyzed for the period 1946–1954. Near-resident and juvenile marine migrant species were demersal while all marine seasonal visitors species were pelagic. Based on stomach content composition, the trophic position of four of the various shark and skate species could be reconstructed. The (near)-resident species, the lesser spotted dogfish, the marine juvenile migrant, the starry smooth hound, and the benthopelagic marine seasonal visitor, the thornback ray, had a benthic/demersal diet (polychaetes, molluscs and crustaceans), while the pelagic marine seasonal visitor, the tope shark, fed dominantly on cephalopods and fishes. Diet overlap occurred for fish (tope shark and lesser spotted dogfish), for hermit crabs (lesser spotted dogfish and starry smooth hound) and for shrimps (thornback ray and starry smooth hound). Trophic position ranged from 3.2 for thornback ray preying exclusively on crustaceans to 4.6 for the tope shark consuming higher trophic prey (crustaceans and fish). The analysis indicates that most of the shark and skate species were generalist predators. The calculated trophic positions of shark and skate species indicate that those species were not necessarily at the top of the marine ecosystem food web, but they might have been the top predators of their particular ecological assemblage.

Introduction

Worldwide, major structural and functional changes have occurred in coastal ecosystems due to overfishing (Pauly et al 1998; Jackson et al 2001; Lotze 2005). Pauly et al (1998) state that this so-called "fishing down the marine

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food web" reflects the removal of long-lived, high trophic level, piscivorous fish, including sharks and skates. It is unclear what effect the removal of top predators can have on the stability of a community (Shurin et al 2002), because for instance the relationship between food chain stability and food chain length is unclear (Sterner et al 1997). While it is easy to predict that carnivores have a high trophic position and exert a degree of top-down effects, these effects are still very poorly understood (Cortés 1999). Consequences of the removal of top predators could have a cascading effect down the food web, through to lower trophic positions such as bivalves and polychaetes (Hussey et al 2015). These cascades potentially could extend to the level of the primary producers (Myers et al 2007). Considering these possible consequences, eliminating larger predators carries more risks of broader ecosystem degradation than previously thought. Top down effects must be widely expected whenever entire groups of predators are eliminated or removed.

The loss of top predators will cause a reduction of the mean trophic level in fish communities (Estes et al 1998; Worms and Myers 2003; Dulvy et al 2004; Frank et al 2005; Myers et al 2007), but the impact can vary across niches and communities (Borer et al 2005; Frank et al 2007). Predator reductions can also cause a shift in niche availability, which can subsequently alter the niche of other predatory species (Frid et al 2007). As top predatory species, sharks and skates might play pivotal roles in the regulation of lower trophic level organisms and, therefore, of marine ecosystems (Myers et al. 2007). For instance, model studies on the impact of shark depletion in different ecosystems showed differences in the response of prey species and a larger increase in the abundance of minor prey species compared to major prey species (Stevens et al 2000).

Whereas sharks and skates used to be more common in the North Sea and surrounding coastal areas, nowadays these species are one of the most vulnerable groups of marine fishes (Dulvy et al. 2004; Stevens et al. 2000) and are under pressure and either absent or occurring in low densities (de Vooys et al 1991; Walker and Heessen 1996; Walker and Hislop 1998; Heessen et al 2015; Bom et al. 2020). For instance, the thornback ray *Raya clavata* was a common species in Dutch coastal waters, but has disappeared from the late 1950s onwards (Walker and Heessen 1996). The trophic position of the species that are still present in the North Sea indicate also a relatively high trophic position (Jennings et al 2002).

Sharks and skates were common in Dutch coastal waters and estuaries in the past (Egmond 2005). These waters also have been subject to pervasive human disturbance for centuries (Lotze 2005, 2007). A compilation of available information by Witte and Zijlstra (1983) listed ten shark and skate species that were components of the coastal fish community in the past but were already considered extremely rare by the 1970s. For one of the species, the common smooth-hound *Mustelus mustelus* doubt occurred about the taxonomic identification. Heessen et al (2015) state that species identification between the common smooth-hound and the starry smooth-hound (*Mustulus asterias)* has been quite problematic and that the common smooth-hound is not as common as suggested or may not even occur in the North Sea, implying that all identification in the past of *M. mustulus* would have been *M. asterias*. In an update, Wolff (2005) and Bom et al. (2020) concluded that nowadays, additional rare species had become extinct in or near Dutch coastal waters. Conversely, recently commercial catches have recorded the re-occurrence of some shark species in the Dutch coastal zone (source: Sportvisserij (Dutch fishing society); The Netherlands).

FishBase (Froese and Pauly 2019) provide average trophic positions of individual sharks and skates, but these might not correspond with local observations as a recent analysis of the Wadden Sea coastal fish food web by Poiesz et al (2020) has shown. Therefore, the past role and trophic position of these lost sharks and skates in the Dutch coastal zone fish food web is unknown. Recent isotope studies showed that the trophic ecology of shark and skate species is potentially very complex (Hussey et al 2015; Bird et al 2018; Flowers et al. 2020).

The aim of this study is to reconstruct the trophic position for shark and skate species listed by Witte and Zijlstra (1983) in the past food web of the Dutch coastal North Sea zone. This information on the trophic position of these lost ecosystem components is important with respect to our perspective regarding past food web structure and functioning. The reconstruction is based on information on stomach content composition of fish species in the Dutch coastal zone and estuarine Wadden Sea, dating back to the 1930's (de Vooys et al 1991). The data were extracted from the archive of the Royal Netherlands Institute for Sea Research (NIOZ). These reconstructions of the trophic position of different shark and skate species was done in line with a recent analysis of the present fish food web structure in the western Wadden Sea by Poiesz et al (2020).

First, the various shark and skate species were listed according to their mode of life (pelagic, benthopelagic or demersal) following FishBase (Froese and Pauly 2019) and their functional group [marine seasonal visitors, (near)-residents or juvenile marine migrants] after Zijlstra (1983) and Elliott and Dewailly (1995). Next, stomach content and ontogenetic shifts in diet were analyzed and described for the various species. Subsequently, the trophic positions of shark and skate species were reconstructed based on the stomach composition. Since the historical data set only contained information on prey species found, trophic position was estimated based on the average trophic position of the various prey species, ignoring differences in mass between the various prey species. The potential bias of ignoring differences in prey mass was investigated with a recent data set of stomach content data of fish community of the Wadden Sea collected between 2010 and 2018 (Poiesz et al 2020). Lastly, the relative degree of specialization in the diet of the various shark and skate species was reconstructed and dietary overlap among species was quantified and the niche type for each species was determined.

Materials and methods

The NIOZ archive

In the period from 1930 until 1969, trained staff of the Royal NIOZ registered landings of rare fish and invertebrate species. Specimens were delivered at the port of Den Helder, mainly by local fishermen from Wieringen, Texel and Den Helder and were paid for with a price slightly above the auction value at the local market. Most of the landings originated from Dutch coastal North Sea waters and the rest from inside the Dutch Wadden Sea.

All elasmobranchs were identified to the species level. All information about species, date of catch, catch location and depth, size of the fish and stomach content was stored. A detailed description of the NIOZ archive can be found in de Vooys et al (1991, 1993).

Stomach content analysis

Prey items were in most cases identified and registered to species level. When prey items were (partly) digested, identification was made to a higher taxonomic level. Almost all prey items (total of 364) could be identified at least at the class level. In only a few cases unidentified prey items were registered. These were removed from further analysis. For prey species belonging to fishes, shrimps and crabs, total length was also registered. Incomplete specimens, often from species that were eaten in pieces such as *Alitta virens* or *Ensis leei* or when species were in part such as the *Crangon crangon*, were counted only by the number of 'heads'. Nine classes were identified (worms, sea stars, bivalves, gastropods, crabs, shrimps, lobsters, cephalopods and fishes).

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).

Trophic position (TP)

For each prey species, the mean trophic position was taken for their class, order and family as taxonomic group (see Suppl Mat Table A1). FishBase (Froese and Pauly 2019) was used as it provided dietary information of over 800 mostly peer-reviewed references.

Trophic position (TP_j) for each individual skate or shark j, was calculated in line with a previous study of the trophic structure of the Wadden Sea fish fauna (Poiesz et al 2020). as 1 + the mean value of the trophic positions of the different prey species found in a stomach:

$$TP_j = 1 + \sum (\overline{TP}_{i1} + \overline{TP}_{i2} + \overline{TP}_{i3} \dots) \qquad (1)$$

where.

TP_j being the calculated trophic position of the individual predator j;

TP_{i1} the mean trophic position of the first prey species $i1$.

$TP_{i2}, TP_{i3} \dots$ the mean trophic position of the second and third etc. prey species.

Potential bias in trophic position

From the data set of stomach content data of fish community of the Wadden Sea collected between 2010 and 2018 (Poiesz et al 2020), all individual fishes with at least two different prey species were selected. For these individuals ($n = 5300$), trophic position was estimated in two different ways:

Estimate 1: Based on mean trophic position of the prey items in line with this study. Trophic position was calculated as 1 + the mean trophic position of the various prey species according to FishBase.

Estimate 2: Based on weighted mean trophic position of the different prey masses. First, the 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, whereby for small prey items a mean wet mass was taken. Next the trophic position of the predator was estimated as 1 + the weighted average of the trophic positions of the various food items.

Table 1 List of shark and skate species extracted from the NIOZ archive

Group	Scientific name	Common name	Trophic position FishBase ($\overline{TP}$)	Mode of life	Functional group
Sharks	*Alopias vulpinus*	Common thresher	4.6 (± 0.0 SE)	Pelagic	MSV
Sharks	*Lamna nasus*	Porbeagle	4.6 (± 0.0 SE)	Pelagic	MSV
Sharks	*Cetorhinus maximus*	Basking shark	3.4 (± 0.3 SE)	Pelagic	MSV
Sharks	*Scyliorhinus caniculus*	Lesser spotted dogfish	4.01 (± 0.3 SE)	Demersal	NR
Sharks	*Mustelus asterias*	Starry smooth-hound	3.88 (± 0.3 SE)	Demersal	JMM
Sharks	*Galeorhinus galeus*	Tope shark	4.37 (± 0.1 SE)	Benthopelagic	MSV
Sharks	*Squatina squatina*	Angelshark	4.33 (± 0.5 SE)	Demersal	JMM
Skates	*Raja clavata*	Thornback ray	3.59 (± 0.2 SE)	Demersal	JMM
Skates	*Dasyatis pastinaca*	Common stingray	3.48 (± 0.63 SE)	Demersal	MSV

The average trophic positions ($\overline{TP}$) and the mode of life were extracted from FishBase (Froese and Pauly 2019). Functional group according to Witte and Zijlstra (1983). *MSV* marine seasonal visitor; NR: (near)-resident species, *JMM* juvenile marine migrants

The potential bias associated with not taking prey mass into account was assessed by constructing a linear regression between both estimates.

Niche overlap

To determine the relative degree of specialization in diet and to compare the diets between the different shark and skate species, the Levins' index of niche breath was used (Levins 1968). For this analysis the contribution of each different prey species within a stomach was used and calculated according to:

$$P_{ij} = \frac{N_{ij}}{N_{jtot}} \quad (2)$$

where

P_{ij} being the proportion of each prey species i in the diet of each individual predator j;

N_{ij} the number of individuals of the species i in the stomach of the predator j;

N_{jtot} the total number of preys counted of each individual predator j.

Next, the average proportion (P_{ij}) of each prey species was taken for each predatory species.

In order to compare the different diets, the average proportion of the different prey items (p_{ij}) were classified up to the highest taxonomic level (order) level. Next, Levins' standardized measure of niche breadth (B_j) was calculated according to:

$$B_j = \frac{1}{\sum Pij^2} \quad (3)$$

Levins' measure of niche breadth can range from 1 (indicating a highly specific diet with only one prey species) to < 1 (indicating a less specific diet with more prey species).

To quantify dietary overlap, the MacArthur-Levins' method was used (MacArthur and Levins 1967; Feinsinger et al 1981). It estimates the extent to which the prey of consumer species K overlaps with that of species J. For instance, if species J specializes on a certain type of food source which is also eaten by a more generalist species K, then from species J's viewpoint its niche overlaps completely with the other species, but from species K's viewpoint the niche only partially overlaps with the niche of species J. Therefore, the calculated values can differ between J and K and vice versa. The MacArthur-Levins' method is calculated using the following equation:

$$M_{jk} = s\frac{\sum p_{ij} * p_{ik}}{\sum p_{ij}^2} \text{ and } M_{kj} = s\frac{\sum p_{ij} * p_{ik}}{\sum p_{ik}^2} \quad (4)$$

where

M_{jk} and M_{kj} are the degree of overlap on species j by species k and vice versa, and p_{ij} and p_{ik} are the proportions that food resource i contributes to the diets of species j and k, respectively (Ellis 1996; Sa-Oliveira et al 2014).

Data exploration and visualization

The data was explored using the protocol described in Zuur et al (2010). Ontogenetic shifts in diet and trophic position were explored with length as categorical variable. Local Polynomial Regression (LPR) were used by means of LOESS (span = 0.75) with the ggplot package (Wickham 2016).

Visualizations of the network data was made by the bipartite package in Dormann et al (2009) and Levins' index of niche breath calculation was made using the MicroNiche package (Finn 2020). All further data analysis and data manipulations were done in R (R Core Team 2019).

Results

Species composition

The NIOZ-archive contained information from nine shark and skate species (Table 1). No records were found from the common smooth-hound. Therefore, all records have been considered to have been starry smooth-hound *Mustelus asterias*. One species, the lesser spotted dogfish, belonged to the (near)-resident species and three species were juvenile marine migrants: the thornback ray, the starry smooth-hound and the angelshark. All other species were marine seasonal visitors. (Near)-resident and juvenile marine migrants were demersal species, and all marine seasonal visitors were pelagic species.

Capture locations of individual sharks and skates could be grouped into wider geographical areas (e.g., banks, grounds and holes) in the North Sea and Wadden Sea (Fig. 1). The lesser spotted dogfish, starry smooth-hound, tope shark and thornback ray were captured at almost all locations. All other species were caught throughout the North Sea and Wadden Sea (Fig. 1). The only species that did not occur in the Terschelling Bank was the common thresher shark, while only the starry smooth-hound and tope shark occurred in the eastern Wadden Sea.

Most stomach content data were collected between 1946 and 1954, therefore the analysis was restricted to this period. For five species (common thresher shark, basking shark, common sting ray, porbeagle and angelshark), the NIOZ archive contained very few data, i.e., information from less than ten stomachs (see Suppl Mat Table B1). Therefore these species were not included in subsequent analysis.

Fig. 1 Catch location in the North Sea and Wadden Sea of shark and skate species extracted from the NIOZ archive. The names corresponds with the locations are given below. The numbers of the locations in the table correspond with the numbers in the map. Grey: North Sea locations; black: Wadden Sea locations; white no records
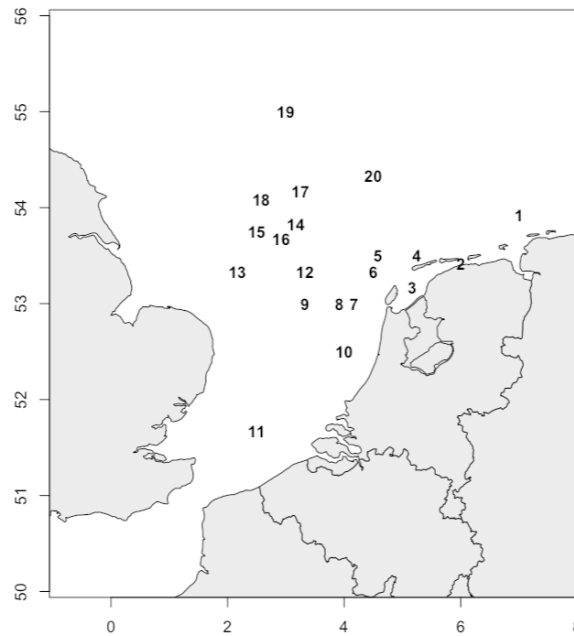
| Location	Name	Alopias vulpinus	Lamna nasus	Cetorhinus maximus	Scyliorhinus caniculus	Mustelus asterias	Galeorhinus galeus	Squatina squatina	Raja clavata	Dasyatis pastinaca
1	Borkummer Stones				grey	grey			grey	
2	Eastern Wadden Sea				grey	black	black			
3	Western Wadden Sea	black	black		black	black	black	black	black	black
4	Terschelling Bank		grey	grey	grey	grey	grey	grey	grey	grey
5	Frisian Front				grey	grey	grey		grey	
6	Vlieland Ground				grey	grey	grey		grey	
7	Texel Hole				grey	grey	grey		grey	
8	Texel Ground	grey			grey	grey	grey		grey	
9	Brown Bank				grey	grey	grey		grey	
10	The Broad Fourteen	grey			grey	grey	grey		grey	
11	Southern North Sea				grey	grey	grey		grey	
12	Tea Kettle Hole				grey	grey	grey		grey	
13	Leman Ground				grey	grey	grey		grey	
14	Botney Cut				grey	grey	grey		grey	grey
15	Markham's Hole				grey	grey	grey		grey	
16	Botney Grounds	grey			grey	grey	grey		grey	
17	Cleaver Bank				grey	grey	grey		grey	
18	Silver Pit				grey	grey	grey		grey	
19	Doggers Bank				grey	grey	grey		grey	
20	Oyster Ground				grey	grey	grey		grey	

Stomach content and trophic position

Lesser spotted dogfish (*Scyliorhinus canicula*)

The size of the lesser spotted dogfish ranged from 10 to 83 cm total length and they were caught in depths between 2 and 77 m. Suppl Mat Fig. B2 shows the records at the various locations. Stomach data from 180 individuals were available: of these 19 stomachs were empty (10.6%) and for 12 stomachs the information about total fish length was lacking. In total 29 different prey items were found (Suppl Mat Table B2), with only a few groups occurring frequently in the stomachs: Pisces and Malacostraca and to a lesser extent Caenogastropoda and Polychaeta. Pisces consisted mainly of Pleuronectiformes (flatfishes, flounder, sole), Ammoditidae (greater sandeel), and Trigiidae (gurnard). Malacostraca included mainly Crangonidae (shrimps), Anomura (hermit crabs) and Brachyura (crabs). Caenogastropoda comprised Buccinidae (whelks) and Polychaeta Annelidae (Nereididae) (Fig. 2). About half (48.4%) of the prey items in the stomachs were crustaceans. With increasing fish size, the occurrence of Brachyura decreased. The occurrence of Annelids (Nereididae) also decreased with size and they were absent above 60 cm in size. Larger lesser spotted dogfish did also
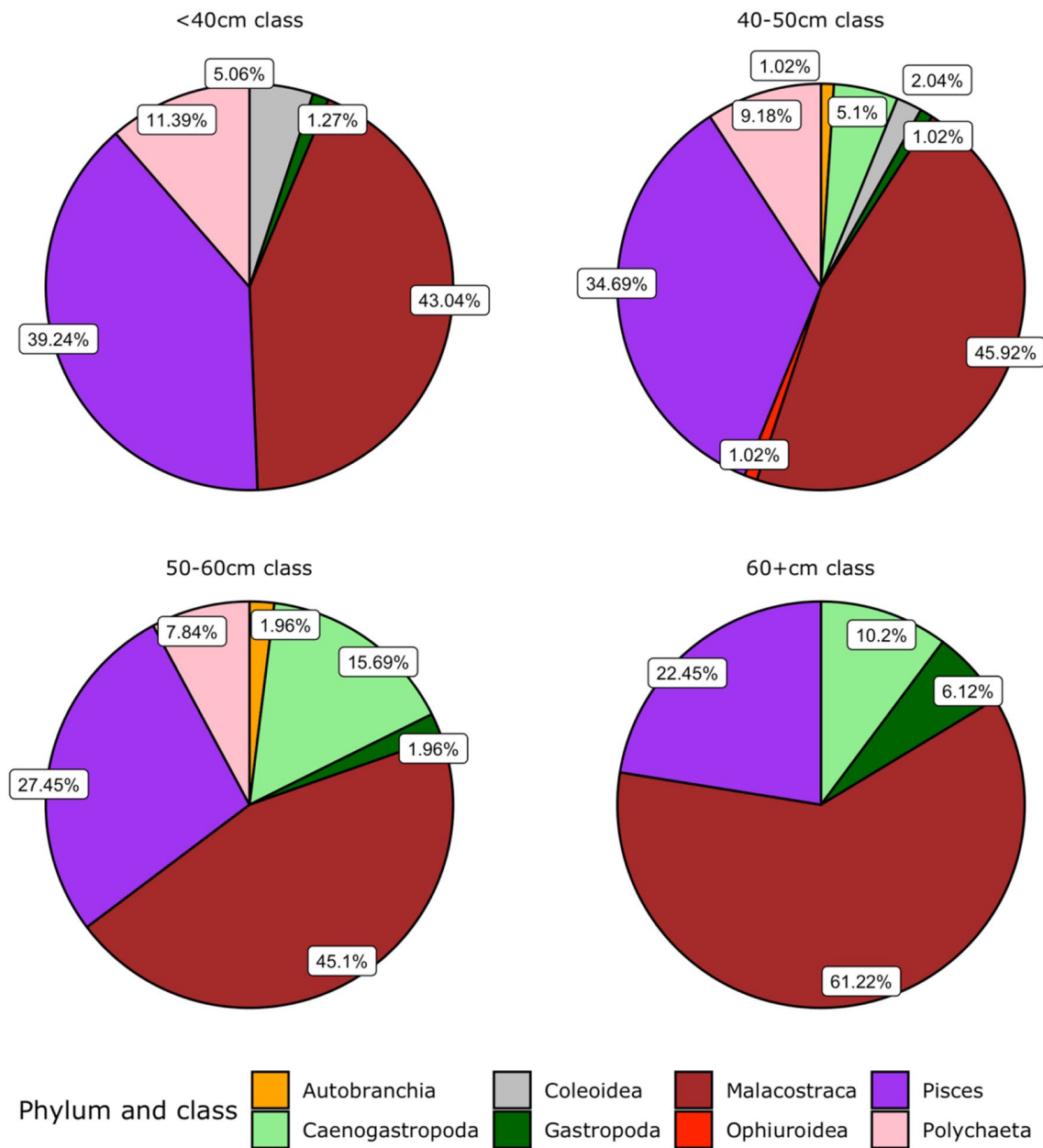
Fig. 2 Occurrence of each prey phylum and class (%) in the stomach of the lesser spotted dogfish (*Scyliorhinus canicula*) for different size classes (cm) between 1946 and 1954

consume flatfishes (Fig. 2). There was variability in the estimates of trophic position, but there was no significant relationship with fish size [ANOVA; $F(3, 149) = 1.492$, $p = 0.22$] (Fig. 6). Mean trophic position was 4.01 (± 0.43 SE).

Thornback ray (*Raja clavata*)

All thornback rays were caught from water depths ranging from 3 to 49 m and measured from 10 to 85 cm in total length. Suppl Mat Fig. B3 shows the number of individuals caught at the various locations. From all thornback rays

captured, 174 individuals contained information about stomach content. Ten individuals (5.5%) had empty stomachs, and for 9 individuals no fish size was documented (Suppl Mat Table B3). The diet of thornback rays mainly consisted of Malacostraca and low percentages of Pisces and some Bivalvia and Polychaeta (Fig. 3). The Malacostraca included mainly Crangonidae (shrimp species) and Brachyura (crab species) and the Pisces were Ammoditidae (greater) sandeel). Nereididae were the dominant Polychaeta family. No trends between trophic position and size was found [ANOVA; $F(3, 152) = 0.892$, $p = 0.447$], which might partly

Fig. 3 Occurrence of each prey phylum and class (%) in the stomach of the thornback ray (*Raja clavata*) for different size classes (cm) between 1946 and 1954
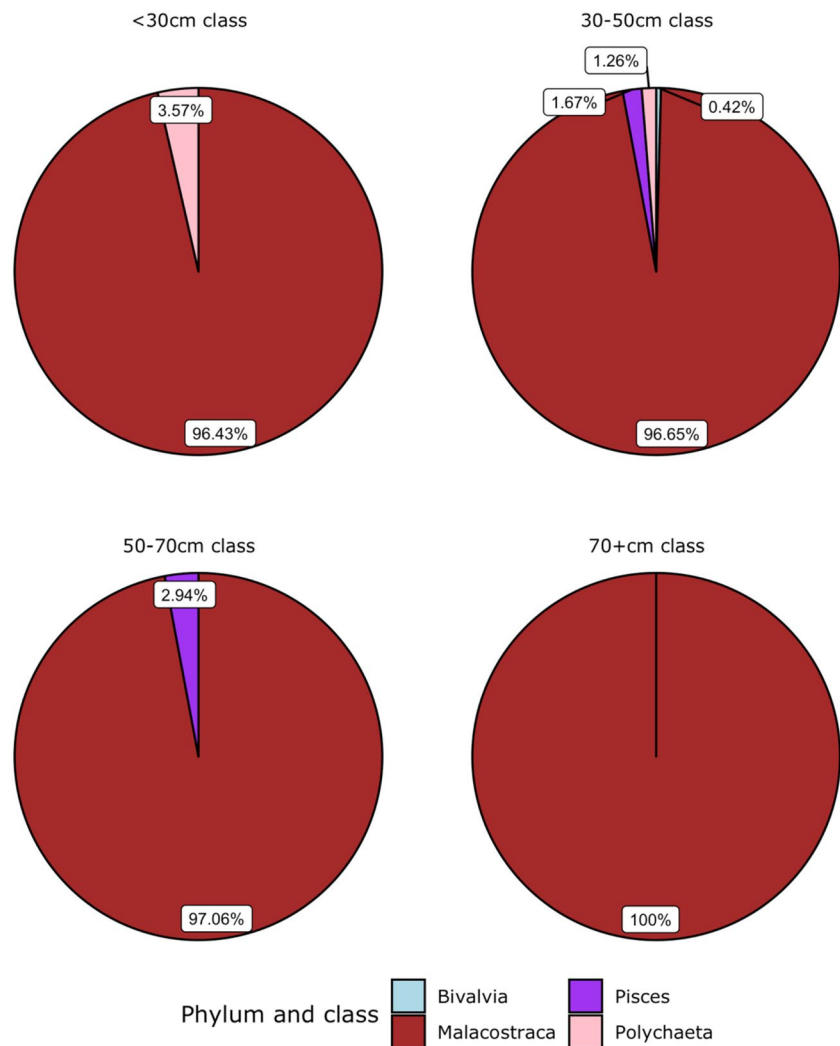
be due to the low number of observations of small (< 30 cm) and large (> 70 cm) fishes (Fig. 6). Mean trophic position was 3.59 (± 0.14 SE).

Starry smooth-hound (*Mustelus asterias*)

Stomach content data of 276 starry smooth-hounds were available. Of these, five individuals (1.8%) had empty stomachs. The total length of the starry smooth-hounds ranged between 27 and 117 cm and they were caught at depths ranging between 5 and 56 m. Suppl Mat Fig. B4 shows the number of individuals caught at each location. Almost all prey species were Malacostraca with in addition some Pisces, Polychaeta and Molluscs (Fig. 4) (See Suppl Mat Table B4 for more detailed information). The Malacostraca were Crangonidae (various shrimp species), Anomura (hermit crabs) and Brachyura (crabs). The few Pisces belonged to the Callionimidae (dragonets) and the Polychaeta were Nereididae. The prey species remained the same with increasing fish size, however frequency of occurrence did show some

variability over the different size classes. Estimated trophic position showed some variability but was not related to the different size classes [ANOVA; $F(3, 276) = 0.428, p = 0.73$] (Fig. 6). Mean trophic position was 3.88 (± 0.27 SE).

Tope sharks (*Galeorhinus galeus*)

The NIOZ archive contained stomach data of 508 tope sharks, but 29 individuals (5.7%) had an empty stomach and for 2 individuals, total length data was not recorded from prey (See Suppl Mat Table B5 for more detailed information). All tope sharks were caught at depths between 3 and 67 m and the total length ranged from 25 to 166 cm. Suppl Mat Fig. B5 shows the number of individuals caught at each location. Pisces were the most important prey item for all size classes (Fig. 5). Smaller individuals (< 40 cm) also had Malacostraca in their stomachs. Other groups were found infrequently: Polychaeta only occurred in the stomachs below 40 cm total length whereas Asteroidea and Ophiuridae were only present in fish with a total length above 120 cm.

Fig. 4 Occurrence of each prey phylum and class (%) in the stomach of the starry smoothhound (*Mustelus asterias*) for different size classes (cm) between 1946 and 1954
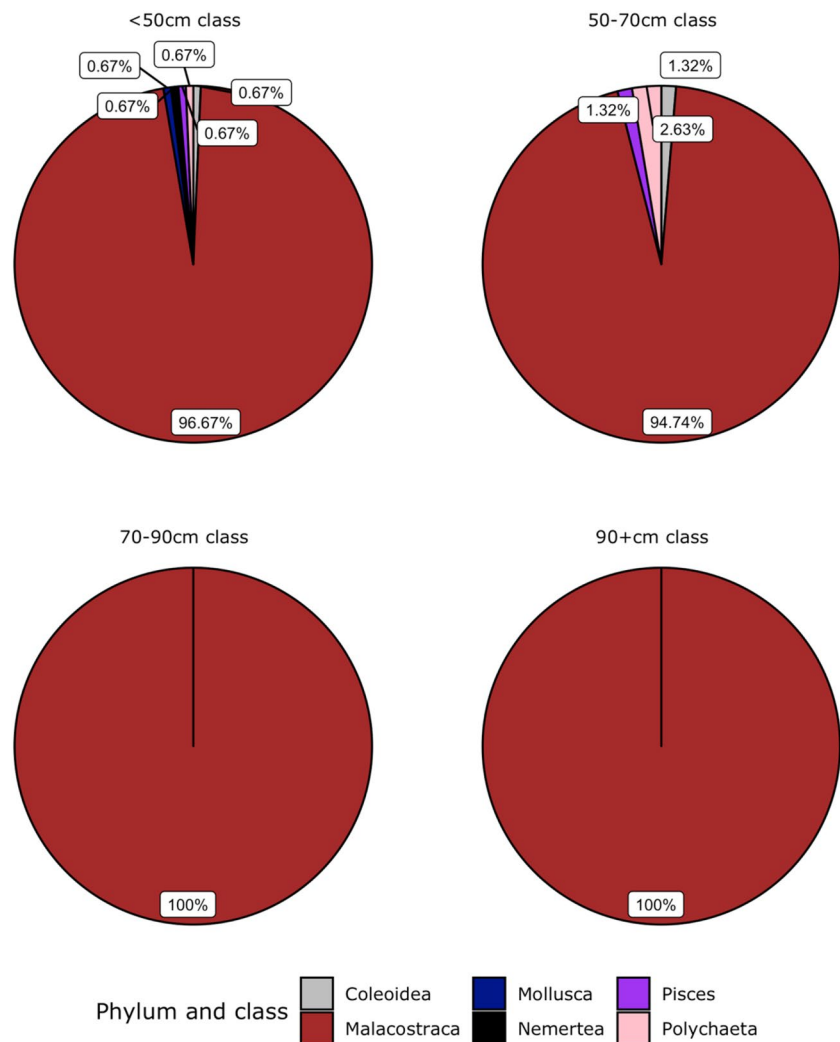
Cephalopods occurred in almost all size classes. Several families of Pisces were eaten: both demersal (Pleuronectidae, Solidae, Gobiidae) and pelagic (Clupeidae, Ammodytidae, Scrombidae, Trigiidae, Tadidae, Carangidae) species. Malacostraca were preyed on mainly by the smallest size groups, especially Anomura (hermit crabs) and Brachyura (crabs) and to a lesser extent Crangonidae (shrimp species). Trophic position showed a significant positive relationship with size [ANOVA; $F(6, 470) = 15.36$, $p < 0.05$], however with some variability (Fig. 6). Overall, mean trophic position was 4.37 (± 0.39 SE).

Other species

Five species (common thresher shark, basking shark, common stingray, porbeagle and angelshark) contained very few data (see Suppl Mat table C1). The diet of the thresher shark consisted mostly of Pisces, while the diet of the basking shark only contained Crustacea. The porbeagle preyed upon Pisces and to a small extend on Cephalopoda. The diet

of the common stingray was more variable and consisted of a mixture of Annelida and Crustacea and some Pisces. The angelshark preyed mainly on Pisces, and in addition on Crustacea and Cephalopoda (Suppl Mat Table C2). Suppl Mat Fig. C1–C5 shows the number of individuals caught at the various locations for these five species.

Potential bias in TP estimate

The data set of stomach content data of fish community of the Wadden Sea collected between 2010 and 2018 contained 2876 stomach content records about 54 prey fish species and 72 different prey taxa. For all individual stomachs, the relationship between the two methods (Estimate 1: based on mean trophic position of the prey items; Estimate 2: based on the weighted mean trophic position of the different prey masses) was highly significant ($R^2 = 0.98$, $p < 0.05$) over a range in trophic positions from 2.0 to 4.7 (Fig. 7). A selection of stomachs containing only fish and crustaceans, corresponding with
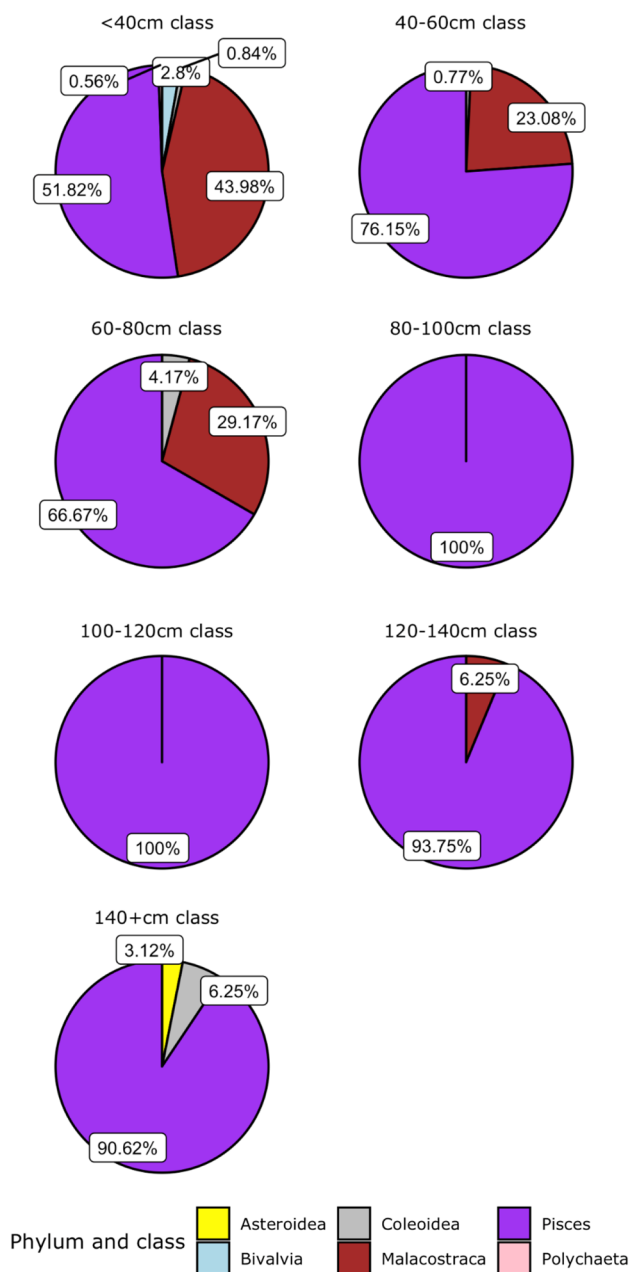
Fig. 5 Occurrence of each prey phylum and class (%) in the stomach of the tope shark (*Galeorhinus galeus*) for the different size classes (cm) between 1946 and 1954

the main prey items of the sharks and skates in this study, resulted in a similar significant relationship ($R^2 = 0.91$, $p < 0.05$; Fig. 7), with an estimated intercept of 0 and slope 95 confidence limits that overlapped with 1. As such, we concluded that no mass-based correction of TP estimates used in this study was required.

Niche overlap

The four shark and skate species appeared to be generalists, feeding on a variety of different prey items (Fig. 8) with differences between the species. The lesser spotted dogfish, the starry smooth hound and thornback ray showed a benthic/demersal diet (polychaetes, molluscs and crustaceans), while the tope shark fed dominantly on cephalopods and fishes. Most diet overlap occurred for three groups of prey: Pisces, Crustacea and Cephalopoda (Fig. 8).

Niche overlap occurred for fish (tope shark and lesser spotted dogfish), for hermit crabs (lesser spotted dogfish and starry smooth hound) and for shrimps (thornback ray and starry smooth hound). A niche overlap analysis (Table 2) showed that the lesser spotted dogfish had a significant diet overlap with the other species. The tope shark showed no significant diet overlap with other predatory species (Table 2).

Discussion

We used historical dietary data to examine the trophic ecology of four species of sharks and skates which have disappeared from Dutch coastal and North Sea waters. Our results show that the four species were generalist feeders and had trophic positions between 3.2 and 4.6. Three species, the (near)-resident lesser spotted dogfish, the marine juvenile migrant starry smooth hound, and the benthopelagic marine seasonal visitor thornback ray had a benthic/demersal diet feeding especially on polychaetes, molluscs and crustaceans. The pelagic marine seasonal visitor tope shark fed dominantly on cephalopods and fishes. The diet of the different species overlapped: for fish (tope shark and lesser spotted dogfish), for hermit crabs (lesser spotted dogfish and starry smooth hound) and for shrimps (thornback ray and starry smooth hound).

The catch data of the various species illustrate that the records of most sharks and skates from the NIOZ archive originated from Dutch coastal waters. These shark and skate species can be considered part of the wider Dutch coastal and Wadden Sea food web as they have also been registered inside the Wadden Sea (Witte and Zijlstra 1983). Tagging experiments also indicate that the data may be representative for the Dutch Wadden Sea. Tagging of the tope shark and the starry smooth-hound has shown migration of these species from the south coast of England and the north coast of Wales to the Bay of Biscay in Portugal (Holden and Horrod 1979; Farrell et al 2010). Also, thornback rays move over several hundred kilometers (Walker et al 1997) and the lesser spotted dogfish have shown movement up to 30 kms (Rodríguez-Cabello et al 1998, 2004; Sims et al 2001). The movement of the common stingray has not yet been studied,
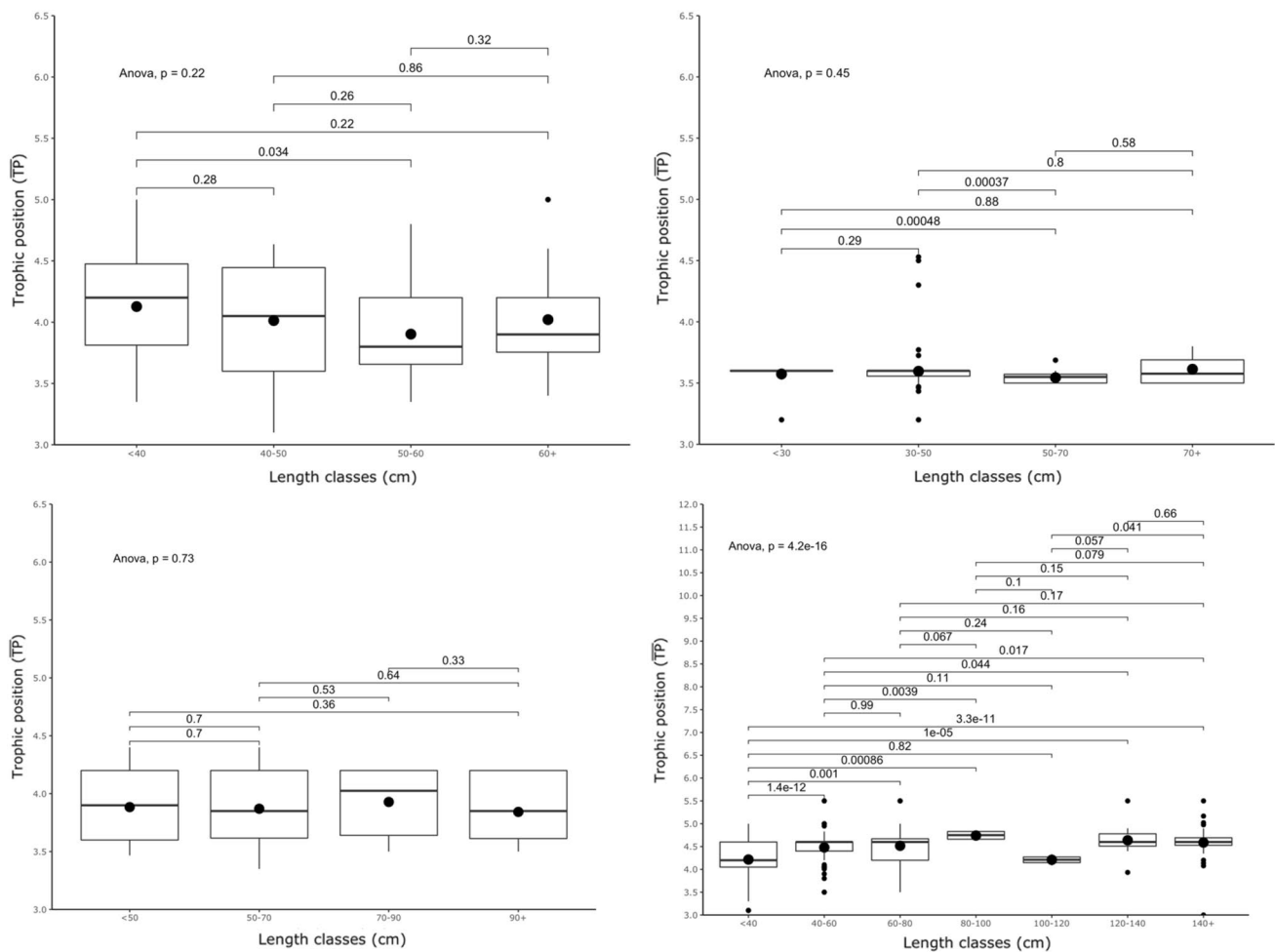
Fig. 6 The average trophic positions ($\overline{TP}$;–) based on stomach content composition related to boxplot length classes (cm) with whiskers, black dot as mean for each length class and *p* value for comparison between echt length class. Top left: the lesser spotted dogfish (*Scyliorhinus canicula*); Top right: thornback ray (*Raja clavata*); Bottom left: starry smooth-hound (*Mustelus asterias);* Bottom right: tope shark (*Galeorhinus galeus*)

but the dispersion of this species as shown in de Vooys et al (1991), indicates a population that lived close to or in the Dutch Wadden Sea.

Diet composition

The taxonomic identification of the stomach contents in this study was not always made to species level but to higher taxonomic groups (class and order). More detailed information may have resulted in more detailed information about segregation and overlap in prey items between species. Also, elasmobranchs quickly digest and break down their prey (Córtes et al. 2008; Wieczorek et al 2018), which might have meant that soft-bodied prey were under-represented.

Due to the limited data available for five species (the common thresher shark, porbeagle, basking shark, the angelshark and the common stingray), it is questionable whether these species are really generalist or specialist feeders. At least for

the angelshark*,* the focus on crustaceans and (flat) fishes in the Irish Sea (Ellis et al 1996) suggest that this species is a specialist feeder. The other four shark and skate species in the Dutch coastal zone appeared to be generalist predators consuming a variety of polychaetes, mollusks, crustaceans and teleosts, as also found for the North-eastern Atlantic by Ellis et al (1996). In generalist predators, spatial differences in diet composition might be expected reflecting local variability in prey availability.

In the Dutch coastal zone, the diet of the lesser spotted dogfish contained a wide variety of other taxonomic groups but about half of the prey items were crustaceans, similar to reports from other parts of the North Sea (Pinnegar 2014) and elsewhere (Lyle 1983; Ellis et al 1996; Wieczorek et al 2018). The diet of thornback rays in the Dutch coastal zone mainly consisted of crustaceans and low percentages of Pisces and some Bivalvia and Polychaeta. The diet composition of the starry smooth-hound contained
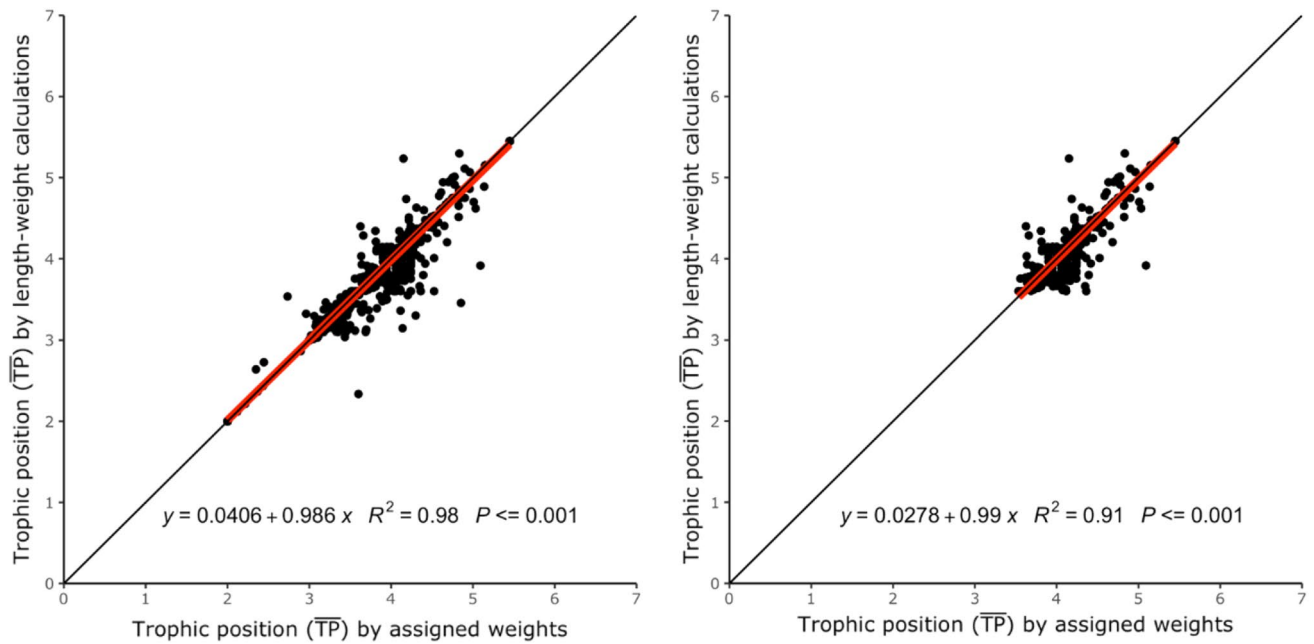
Fig. 7 Relationship between two estimates of trophic position (TP) based on stomach content data. X axes: TP calculated based on the mean of the trophic positions of the different prey items. Y axes: TP calculated based on the weighted mean of the trophic positions of the prey items after reconstruction of their mass. The black line represents the y = x. Left panel: all individual data of 27 species. Right panel: all individual data with TP > 4. Data after Poiesz et al. (2020)
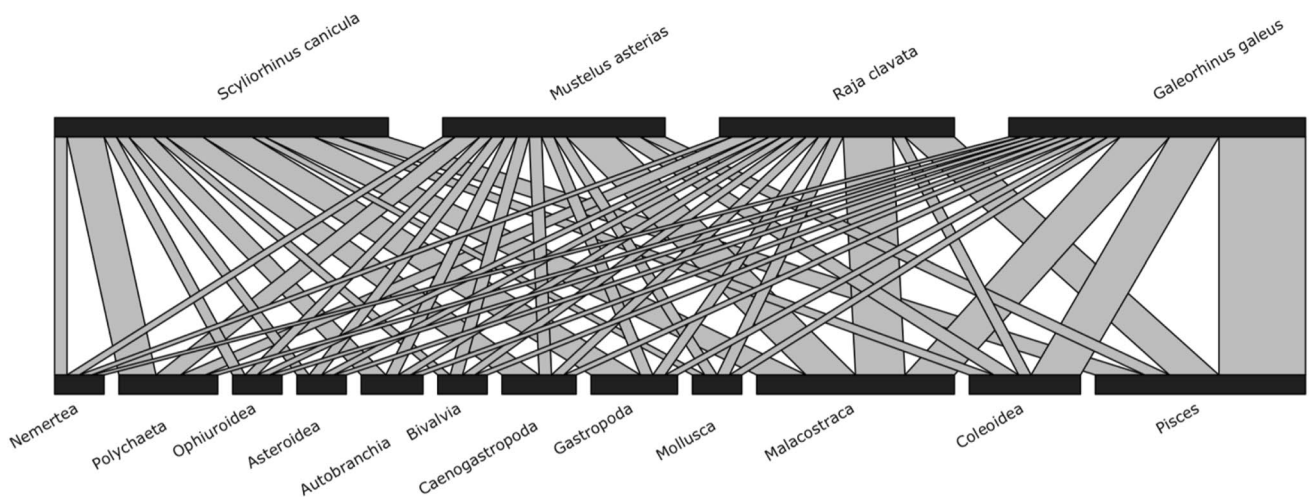
Fig. 8 Network analysis based on the overlap in occurrence of prey species in the stomach of the various shark and skate species. Prey classes are listed from lowest average $\overline{TP}$ to highest average $\overline{TP}$

Pisces and Crustacea and to a lesser extent Caenogastropoda and Polychaeta. The focus of both species on mainly crustacean species is comparable with feeding patterns in other parts of the North Sea (Daan 1993; Pinnegar 2014). Other studies reported similar diet composition for the common stingray, but also included additional benthic invertebrate species (Yeldan et al 2009; Saglam et al 2010; Šantić et al. 2011). The diet composition of the starry smooth-hound also corresponded with the findings of Ellis et al (1996) for the Irish Sea, but the NIOZ archive data showed an additional consumption of shrimps in the early life stage. The results for the tope shark found in this study are in line with the those described for sharks by Cortés (1999).

In this study, ontogenetic shifts in diet were only found the lesser spotted dogfish and the tope shark whereby the prey size and diet composition differed with total length and

Table 2 MacArthur and Levins' measure of niche overlap for the shark and skate species from the NIOZ archive between 1946 and 1954

Species	Scyliorhinus caniculus	Raja clavata	Galeorhinus galeus	Mustelus asterias
Scyliorhinus caniculus		0.666**	0.914**	0.671**
Raja clavata	0.495		0.261	0.998**
Galeorhinus galeus	0.562*	0.486		0.469
Mustelus asterias	0.494	0.998**	0.253	

Values are indicating the extent to which the diet of species (X) is overlapped by the diet of species (Y). Significance: ** $p \leq 0.05$; *: $0.05 < p < 0.10$. Values from 0.6 are considered to indicate significant niche overlap

life stage, in line with other studies (Lyle 1983; Ellis et al 1996; Henderson and Dunne 2002; Lucifora et al 2006; Martinho et al 2012). In the lesser spotted dogfish, the occurrence of crab and polychaeta worms decreased with size while in the tope shark smaller individuals (< 40 cm) had crustaceans in their stomachs and larger individuals had a wider variety of fish species (Pleuronectiformes, Gadidea). Ontogenetic shifts in diet have also been described for the thornback ray in contrast to this study. In other areas, young individuals prey on small crustaceans such as shrimps, while larger individuals consume larger crustaceans, such as swimming crabs (Holden and Tucker 1974; Ellis et al 1996; Farias et al 2006). In this study, only large thornback rays > 70 cm showed a higher preference for Pisces.

Trophic position

Estimates of trophic position might to some extend depend on the methodology used. In a previous analysis of stomach contents of the lesser spotted dogfish from the west coast of Ireland, Wieczorek et al (2018) found mainly hard-bodied prey or vertebrates, such as decapods or fish with a relatively higher trophic level. However, a simultaneous stable isotope analysis resulted in a lower estimate of the trophic position of the lesser spotted dogfish (Wieczorek et al 2018). Apparently, elasmobranchs digest soft-bodied prey items very quickly and therefore their contribution is underestimated by stomach content analysis. Conversely, comparable trophic positions estimated from isotope composition were found by Jennings and van der Molen (2015) for the two species in this study (the thornback ray and the starry smooth-hound). This suggests that estimates of trophic position based on historical stomach content data may be biased due to missing digested soft prey items. In this study stomachs with a record of only a single prey item resulted in some cases in an estimate of a very low or high trophic position of the predator. Most likely other less important prey items were not registered or identified in these stomachs and as such, estimates of trophic position based on these data are invalid. However, stomach content analyses remains a simple and valuable tool to reconstruct the historic trophic position of predators, including predator–prey relationships and niche

overlap. For future studies, it is highly desirable that stomach content analysis and stable isotope analysis should be combined to unravel the complex trophic ecology of these elusive predators (Cortés 1999; Flowers et al. 2020).

The shark and skate species from the Dutch coastal zone also occurred in large parts of the North Sea (Heessen et al 2015) and included species from different functional groups (Zijlstra 1983; Elliott and Dewailly 1995). One species, the lesser spotted dogfish, belonged to the (near)-resident species and three species were juvenile marine migrants: the thornback ray, the starry smooth-hound and the angelshark. All other species were marine seasonal visitors. (Near)-resident and juvenile marine migrants were demersal species, and all marine seasonal visitors were pelagic species. Most niche overlap occurred among the benthic/demersal species for hermit crabs (lesser spotted dogfish and starry smooth hound) and for shrimps (thornback ray and starry smooth hound). There was no evidence for overlap between the lesser spotted dogfish, starry smooth-hound and thornback ray. The pelagic tope shark had some overlap for fish with the benthic/demersal lesser spotted dogfish.

Estimates of trophic position ranged from 3.2 for thornback ray preying exclusively on crustaceans to 4.6 for the tope shark consuming higher trophic prey (crustaceans and fish) over the period 1946–1954. The calculated trophic position for the shark and skate species in the Dutch coastal zone in this study corresponds closely with that found in other parts of the North Sea by Jiming (1982). The calculated trophic positions of shark and skate species indicate that some species fed at the top of the marine food web, but others fed at a lower trophic level, but may be top predators of their ecological assemblage.

Past role in the food web

Common thresher, porbeagles, basking and angel sharks have been extremely rare for a long period in the Dutch Wadden Sea and coastal area (Witte and Zijlstra 1983; Heessen et al 2015). As such, predation pressure and potential food competition from these species will have been low for decades. Commercial landings of skates and rays in the past (Heessen et al 2015; Bom et al. 2020)

indicate substantial densities in the Dutch coastal zone at that time and imply that they were an important component of the past food web and that their disappearance might have caused changes in the community through competitive release as stated by Stevens et al (2000).

The effects of removing large numbers of these top predators on the marine ecosystem is still largely unknown (Stevens et al 2000), but might be substantial for Dutch coastal waters. For instance, Lynam et al (2017) suggest that top-down exploitation of predators has an important effect on the dynamics of other fish populations and can initiate complex cascading effects. In the North Sea especially planktivorous (top) predators should play such a central role (Lynam et al 2017).

A recent analysis of contemporary food web structure of the Dutch coastal fish community based on stomach content analysis resulted in trophic positions between 2.0 and 4.7, with most trophic positions above 3.0. Until a few decades ago, (near)-resident species were the most abundant functional group in spring and juvenile marine migrants in autumn (Poiesz et al 2020). Part of the shark and skate species analyzed in the study also belonged to (near)-residents and marine juvenile migrants. Therefore, coastal zone habitats were likely more important for (near)-residents and marine juvenile migrants in the past than nowadays.

The various shark and skate species differ with respect to their prey location, prey depth, prey size and feeding times (Young et al 2010). Mouth dimensions of skates correlate with their diet and prey specialization (Walker 1998; Scharf et al 2000). This trophic or behavioral separation also causes niche segregation. Our work has shown that these now rare species likely played important trophic roles in Dutch coastal waters. However, to what extend these species can be considered as top predators within their own ecological assemblage (Pusineri et al 2008; Young et al 2010), is still unknown. For instance, some reportedly "top-predator" species such as skates (thornback ray), feed at a relatively low trophic position and prey to other species with a higher trophic position (Flowers et al. 2020).

Declarations

Conflict of interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Ethical approval Human and animal rights statement: This article does not contain any studies with animals performed by any of the authors.

Consent to participate All authors declare that they give consent to participate.

Consent for publication All authors declare that they give consent for publication.

Availability of data, materials and code All data, materials used, and code will be available on request.

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