Ecomorphology as a predictor of fish diet: a case study on the North Sea benthic fish community.

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SUMMARY

A methodological approach based on fish ecomorphology was chosen to predict potential fish diet. This study tests a method used in earlier research on a marine ecosystem containing phylogenetically diverse organisms: the North Sea. Fish feeding morphology imposes constraints on feeding options. A bottom-up perspective was used to describe the demands that food makes on fish feeding morphology. A set of quantitative morphological variables were measured on fish and compared to the demands made by different food-categories. Common North Sea Gadiformes and Pleuronectiformes were analysed. The results of the measurements were used as a basis for predictions of potential diet. Five ‘morphotypes’ were identified: *Large-mouthed flatfish*, *small-mouthed flatfish*, *soles*, *ling/rockling/haddock* and *other Gadiformes*. The predictions on diet were checked by stomach content data from literature. The main conclusions were that morphology differed significantly among fish species indicating detailed morphological adaptations to specific food types. Furthermore the utilization of fast, relatively large prey were predicted better than the utilization of slow or sessile prey that is well hidden, hard to crack or otherwise ‘tough to handle’. Also the method failed to clearly separate different food types within this group of fast/large prey. Moreover, no clear distinction in stomach contents were found between *Large-mouthed flatfish* (being predicted as eating mostly shrimp) and *Gadiformes* (being predicted as eating mostly fish) within the group of fast prey hunters. Overall predictions succeed in separating different feeding guilds, but in some cases do not succeed in distinguishing between species. Knowledge on feeding behaviour on slow and sedentary benthic prey is a limiting factor. Also limiting the usefulness of the study is the incomplete knowledge and/or implementation of this knowledge on the distribution of both benthic fish and benthic prey items.

1 INTRODUCTION

Fisheries are an important source of human food. Ecological knowledge is required to describe aquatic ecosystems in order to understand the effects of fishing on the ecosystem structure and functioning. Most commercially important fish stocks in developed fisheries, such as in the North Sea, are intensively monitored to form an image of the communities present, and how fished species may react on fishery pressure. Food webs are reconstructed to understand feeding relationships and hence energy flow is determined by the abundance of the various fish species, their habitat requirements and feeding characteristics (Greenstreet et al. 1997; Heath 2005; Jones 1982; Jones 1984; Steele 1988).

A direct and common approach to determine fish diet is to examine stomach contents of fish (e.g. Table 5). While it is a reliable way of determining what fish eat, it results in information on the *actual* diet at the time and place of sampling only. Therefore it is suited to explain e.g. diurnal differences (Albert 1995; De Groot 1971) and seasonal variability in diet (Rae 1965), but it does not allow generalized conclusions on what a species *can* eat. The method is also labour-intensive, since reliable results require a great amount of samples over time and space, because of large intra-specific variation in diet (Arntz 1971; Rae 1965).

An alternative method, based on fish morphology, approaches fish diets from a different angle. When studying functional fish feeding morphology both potentials and constraints on feeding options are apparent (De Groot 1971; Keast and Webb 1966; Piet et al. 1998; Sibbing and Nagelkerke 2001). This principle of predicting ecological traits such as potential diet from (functional) morphology is ecomorphology (Findley and Black 1983; Gatz 1979; Motta 1988; Wainwright 1988). The main difference with the stomach analysis method is that fish diet is not 'observed', but *predicted.* This means that it gives a generalized view of *potential* diet and that questions may be asked such as: do fish use their full diet potential at a given point in time and space; do they expand or change their feeding niche if the abundance of a dominant competitor changes due to fishing pressure? Elucidating these potentials is what makes this method valuable.

Sibbing and Nagelkerke (2001) applied the ecomorphological method on a cyprinid species flock in Lake Tana, Ethiopia to predict potential diets of the fish to clarify resource partitioning among the investigated species. Their approach to assess potential diet was based on the definition of food properties and the consequent demands that food makes on functional feeding morphology. The feeding morphology was quantified by a set of measurable morphological variables that determine the total feeding process, so both foraging and internal food processing. The extent, to which the morphology of a particular species matched the demands for utilizing a particular food type, was used as an index for the suitability of a species to utilize a particular food resource. The aim of this research is to apply this same approach to a phylogenetically diverse fish community. Is the method also efficacious in cases other than a species flock in an isolated freshwater lake? Does this method provide sufficient resolution to make predictions within the category of benthic food types? The fish community chosen to test this is that of the

North Sea. There are several reasons that support the choice of the North Sea as a case study:

1) According to Daan et al. (1990), 224 fish species can be identified in the North Sea, that belong to over 50 different families (Knijn et al. 1993). The most common in terms of abundance are: *Gadiformes* (cods), *Pleuronectiformes* (flatfish), *Perciformes* (in the North Sea mostly sand eels, mackerel, scad, gobies, weevers and dragonets), *Clupeiformes* (herrings), *Rajiformes* (skates and rays), *Scorpaeniformes* (in the North Sea mostly gurnards and bull routs) and *Squaliformes* (spurdogs). The current study was restricted to 21 bottom- dwelling fish species encompassing 6 families from the 2 most abundant orders: the Gadiformes and the Pleuronectiformes (commonly known as roundfish and flatfish, respectively).

2) There are numerous studies on the feeding ecology and distribution of North Sea fish species that can be used to verify/falsify the predictions from the ecomorphological approach.

3) As the North Sea is heavily fished and substantial changes in the fish assemblage have been documented (Daan et al., 2005; Rijnsdorp et al., 1996), changes in feeding relationships may be explored based on the potential diets inferred from the ecomorphological approach.

The main question of this research is then: can the method developed by Sibbing and Nagelkerke (2001) be used to successfully predict the diets of 21 benthic fish species belonging to 6 different families in a marine ecosystem?

2 MATERIALS & METHODS

This study basically follows the approach of Sibbing and Nagelkerke (2001) with some adaptations. The focus is on the inter-specific differences that are expected to be much higher than the intra-specific differences.

2.1 Ecomorphological approach

The successive steps in the ecomorphological approach are shown in Figure 1.

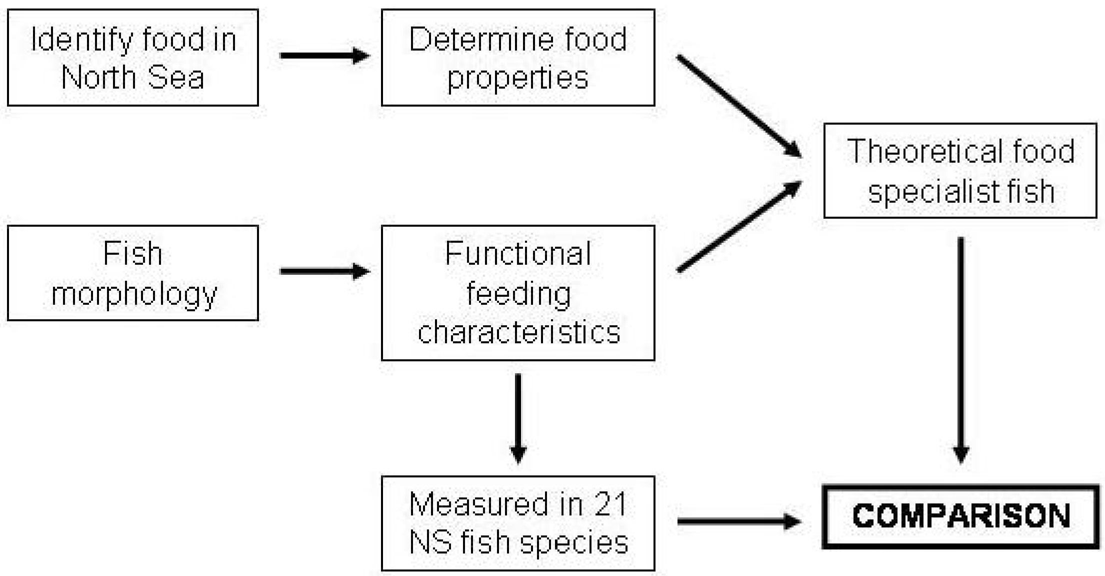

Figure 1. Flowchart describing successive steps in the ecomorphological approach to the feeding ecology of North Sea fish species.

It might prove a challenge to test the model on a phylogenetically diverse group, because morphological characteristics have to be chosen that can be adequately and comparably measured on all different fish species and are indicative of functional feeding morphology.

2.2 North Sea food categories

To obtain a complete spectrum of food available for fish in the North Sea, the original classification (Table 1 in Sibbing and Nagelkerke, 2001) was extended with specific marine prey species based on ‘Tirion gids voor kust en zee’ (Hayward, 1999). After identifying all phylogenetic groups, food properties were scored. The properties from the original table were used but a few changes were made, mostly to replace all descriptions with numerical values.
Changes made are:

- *Maximum diameter:* this property was not used because a choice was made to leave details on size of food types out of the method. One argument for this choice is that food types classified in this research vary greatly in size within their respective categories. A second argument is that because the method takes into account only relative measurements, an absolute prey size would only be useful when compared with an absolute size for the predator. For example: crabs occur in many different sizes, making it impossible to cover the entire category with a strict size. Even if one were to do so, a crab of a certain size would impose different demands on fish of different sizes.
- *Shape:* this was translated into ‘elongate shape’.
- *Major habitat:* was changed into ‘Position in water column’, which describes only in what part of the water-bottom column the food type occurs.
- *Chemical composition:* was divided into 3 separate properties, ‘protein’, ‘carbohydrates’ and ‘indigestible’.
- *Macro- and micro reduction:* these properties were left out because they assume pharyngeal mastication, which is not necessarily applied by all fish species.

2.3 Functional morphological variables of fish

<u>Variable choice:</u>

The first step in the measuring process is the clear definition of measurable fish variables opposing the food variables.
The list developed by Sibbing and Nagelkerke (2001) for cyprinid fish in Lake Tana was altered to describe the North Sea fish species. A list of the variables used is given below. Ideally, more variables would have been used, but due to the limited time only variables that yielded much information at (relatively) low cost in time and/or effort were selected.

Variables from the original list (marked by an asterisk*) as well as new ones are described and arguments from this study or from literature are given for either keeping or discarding it. Variables are divided in groups that each describes a step in the foraging process.

Fish variables and their adaptive value:

SEARCH

- **Orbita length*:** a measure of visual acuity and/or sensitivity. The orbita length is more easily measured than the diameter of the eyeball. However its goal is the same, to quantify visual acuity. Only the size relative to the standard length of the fish was used.
- **Nostril distance:** a measure of smell capacity, a new (try-out) variable. Although the sense of smell in a fish is not easily quantified, it is an important part of the sensory system (De Groot 1971). No references were found that described an easy method of measuring the olfactory sense capacity of fish, however it was deemed worthwhile to try a simple method: measuring the maximum distance between in- and outflow openings of the olfactory organ.
- **Barbel length*:** taste and tactile sense undoubtedly play roles in finding and/or sorting food. In Sibbing & Nagelkerke (2001) taste buds were stained to determine density and to quantify the fishes' capacity for internal taste selection. This was not done in the current research, as it is a time-consuming process. As for external taste, organs containing taste buds are most likely to be located on the snout, barbels, and pectoral- or pelvic fins. The variable was maintained but slightly altered. In this study only the total length of all barbels was estimated, to facilitate comparison among species. This was used as an indicator of external taste. Note that that barbels also give the fish an advantage when feeding at night or in turbid waters (Brawn 1969; Harvey and Batty 2002; Kasumyan and Doving 2003).

APPROACH:

- **Body depth*:** increases the manoeuvrability of the fish, preferable for fish that specialize in a low speed-, fast turning lifestyle often associated with suction feeders, and decreases suitability for a fast swimming lifestyle commonly adopted by open water fast swimmers/predators. Fish with low bodies tend to show a less threatening silhouette as well (Keast and Webb 1966; Webb 1982; Webb 1984).
- **Oral gape area/frontal body area*:** looking in the 'face of the fish', this variable describes what part of the frontal body area the mouth - when fully opened - covers. This variable is important mainly to describe resistance when swimming because the frontal body area is a solid mass creating resistance. Increasing oral gape size reduces this area and thus resistance and reduces the effect of 'pushing away the prey'.
- **% White muscle fibre in tail*:** a variable that shows whether the fish is built for a sprinting (mainly white muscle) or a cruising (meanly red muscle) swimming style.
- **Aspect ratio caudal fin*:** this variable is useful for determining whether the fish is a sprinter or a cruiser. Cruisers have high aspect ratios which mean that they possess high slender caudal fins, whereas sprinters have low aspect ratios defined by low broad caudal fins. (Keast and Webb 1966; Webb 1982; Webb 1984).
- **Caudal peduncle depth*:** the height of the caudal peduncle in the same plane as the caudal fin is used as a third indicator for swimming style. A high peduncle is

beneficial to a sprinter, while a low (narrow) peduncle favours high-speed cruisers (Keast and Webb 1966; Webb 1982; Webb 1984).

INTAKE:

- **Oral gape axis*:** the orientation of the mouth. Some fish have mouths pointing upwards, while others show the opposite. Some food types are easier preyed upon with a certain orientation of the mouth than others.
- **Protrusion length*:** fish that rely on suction/particulate feeding tend to have a large jaw protrusion. In this way their mouths take the shape of a round suction tube. Protrusion is defined as the forward and downward extension of the premaxilla and serves to direct the suction flow and to decrease prey-predator distance at low energetic costs. However in some fish the premaxilla actually tilt upwards (in the Greater sand-eel, *Hyperoplus lanceolatus* for example). As a consequence, not only the abovementioned extension but also the extension of the lower part of the premaxilla was measured. This second measurement was not used however as it would purely describe the orientation of a fully protruded mouth. This is already covered by the variable ‘Oral gape axis’ (Van Dobben 1935).
- **Lower jaw length*:** serves as indicator of how the fish trades off jaw power versus jaw speed and size of mouth opening. A short jaw allows for more powerful biting or scraping (Van Dobben 1935).
- **Hyoid length*:** length of the cerato- and hypohyal bones added together. They form the lower part of the hyoid; the part that rotates around the upper part and that lowers the mouth floor. A longer hyoid bar makes for greater mouth expansion and a greater volume increase; this leads to more suction power (Van Dobben 1935).
- **Opercular sealing flap width:** this is a new (try-out) variable. It measures the maximum width of the sealing flap between the caudal and ventral edges of the operculum and the pectoral girdle. This sealing flap can seal the branchial outlet and allows for a negative pressure build-up in the mouth cavities during (partial) opercular expansion. When the flap is wider it allows for greater (sealed) expansion and thus more suction power.
- **Volume capacity operculum*:** the length of the operculum is divided by its height. A longer, narrower operculum can create a greater volume.
- **Branchial outlet*:** this describes the maximum width of the opening between the operculum and the pectoral girdle. It is an indirect measure of the amount of water passing out through the opercular slits. A fish that needs to swim fast and that has a big mouth must have large branchial outlets to funnel out all the water entering the mouth, at high speed, thus preventing stagnation of the water flow.
- **Gill arch resistance*:** This describes the resistance the gill arch with its gill rakers generates on the water flow through the branchial outlets. Gill arch resistance is the antagonist of ‘branchial outlet’. A fish that needs a *large* branchial outlet (i.e. fast water outflow) also needs *low* gill arch resistance. A high water resistance is not beneficial for any feeding specialist, however what a high gill arch resistance means is that the fish has long and/or many gill rakers, suitable for filtering tiny particles out of the water. Therefore filter-feeding fish ‘need’ a

high gill arch resistance. This variable is useful for it separates filter feeders from hunters (Van den Berg 1993; Hoogenboezem et al. 1992; Kirchhoff 1958).

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- **Maxillar and mandibular teeth types:** this is a new (try-out) variable. One that did not occur in the original article for an obvious reason: cyprinid fishes lack oral teeth. North Sea fish possess a variety of oral teeth, which likely play a role in feeding. Therefore it was desirable to compare the oral teeth among the species. For instance, biting chunks out of relatively solid, static food items requires another type of teeth than restraining a struggling prey fish, or crushing a mussel (Barel et al. 1977; Barel 1983; Fryer et al. 1972; Strait 1997; Witte and Van Oijen 1990).

SIZE SELECTION:

- **Oral gape diameter*:** the difference with the original article is that this variable was not used to determine maximum prey size, as (relative) size is not taken into account in this study. A large oral gape enables the fish to swim fast with less resistance (see 'Oral gape area/frontal body area'), while a smaller gape is more useful for fish that specialize in particulate suction feeding: the smaller mouth increases suction speed, can be aimed more precisely and can access difficult areas more easily.
- **Gill raker length*:** the length of the rakers that can function as a sieve to filter food out of the water. The longer the raker, the greater its potential to filter, but also the higher the resistance it creates (Van den Berg 1993; Hoogenboezem et al. 1992; Kirchhoff 1958).
- **Gill interraker distance*:** measured for the same purpose as 'Gill raker length', interraker distances need to be small when a fish specializes in filter feeding. Resistance increases with smaller distances (Van den Berg 1993; Hoogenboezem et al. 1992; Kirchhoff 1958).
- **Gill raker profile*:** a third variable describing gill-sieve function. Profile is defined as the extent of outgrowths on the rakers. Elaborate outgrowths increase filter capacity and resistance (Van den Berg 1993; Hoogenboezem et al. 1992; Kirchhoff 1958).

TRANSPORT:

- **Postlingual organ width*:** the postlingual organ is the mouth floor between the gill arches. A broad postlingual organ allows for more grip and consequently more efficient transport of large prey items, especially mobile prey. It does limit gill sieve size; therefore filter-feeders indirectly benefit more from a narrow postlingual organ.
- **Pointed anterior pharyngeal teeth*:** pharyngeal teeth might not be as essential for masticating food in North Sea fish as in cyprinids, but they still have a function in transport. Pointed teeth in the front part of the pharynx can hook in to the prey and muscle movements can drag it further into the oesophagus (Barel et al. 1977; Barel 1983; Fryer et al. 1972; Strait 1997; Witte and Van Oijen 1990).

PHARYNGEAL MASTICATION:

- **Type of pharyngeal teeth*:** cyprinids show various different structures that are built for cutting up or crushing larger food particles, therefore the teeth types that were encountered in the species studied in this research were also classified. Sharp, pointed teeth are more suitable in handling soft prey, while molar teeth are better used crushing hard structures.

- **Pharyngeal teeth density:** this is a new (try-out) variable. The density of the pharyngeal teeth on the most caudal tooth plates was measured to compare among species and to see if pharyngeal mastication plays an important role in some species. It was expected that if species use pharyngeal jaws as crushing or tearing tools, the density would be relatively high.
- **Pharyngeal teeth inclination:** this is a new (try-out) variable. The inclination of the teeth is of interest when considering pharyngeal prey diminution: if the upper- and lower teeth are inclined in opposite directions, they might be used to tear prey apart prior to swallowing.

DIGESTION:

- **Gut length*:** the total gut length is a measure for position in the food chain. Piscivores show shortest gut lengths while fish that feed on plant material or detritus have the longest (De Groot 1971; Kramer and Bryant 1995).
- **Stomach size:** this is a new (try-out) variable. Stomach size was classified to see if there were remarkable differences. It is known that piscivorous fish have larger stomachs than fish that forage lower in the food chain (De Groot 1971).
- **Pyloric ceca size:** this is a new (try-out) variable. The number of pyloric ceca and their average size was measured to gain an indicator of the digestive surface they add. Maybe the pyloric ceca perform a distinct digestive function in fish that can be linked to their diet (Buddington and Diamond 1987; De Groot 1971).

Not all new and maintained variables mentioned in the above list were used in the eventual (statistical) analysis. The removal of variables made at later stages is mentioned where appropriate.

2.4 Theoretical food specialists

<u>Specialist fish:</u>

The creation of food specialist fish is essentially an intermediate step that translates the food types into a theoretical fish that is specialized in feeding on that particular food type. Some food types were subdivided into multiple classes of food specialists, because different feeding strategies can be used to exploit them. An example is the food type phytoplankton that was divided into ‘phytoplankton townet feeders’ and ‘phytoplankton pump feeders’. The different food specialists were based on the food properties table earlier and the food specialist table in the article of Sibbing and Nagelkerke (2001). Table 1 shows the transformation of food types into food specialists.

Table 1. Deriving food specialists for particular food categories. A description of the transition of food categories to food specialists. The explanation given for each food specialist describes the feeding mode.

FOOD CATEGORIES	FOOD SPECIALISTS	EXPLANATION
Phytoplankton	phyto-townet feeders	swimming open-mouthed
	phyto-pump feeders	pumping with opercula
Sessile microalgae	algae scrapers	scraping with teeth
Macrophytes/thallous weeds/macroalgae	plant biters	biting at plants
Detritus	detritus feeders	sifting detritus out of bottom
Microzoos	zoo-townet feeders	swimming open-mouthed
	zoo-pump feeders	pumping with opercula
Benthic fish-eggs	egg suckers	particulate suction feeding
Sponges (Porifera)	sponge/anemone/coral biters	biting at sponges
Sea anemones (Anthozoa)	sponge/anemone/coral biters	biting at anemones
Corals (Anthozoa)	sponge/anemone/coral biters	biting at corals
Hydropolyps (incl. moss animals)	polyp biters	biting at polyps
Sea squirts: adult (Ascidiacea)	sea squirt biters	biting at sea squirts
Jellyfish (Scyphozoa)	jellyfish biters	biting at jellyfish
Sea snails: with shell (Gastropoda)	sea snail crushers	crushing shell
Sea slugs: without shell (Gastropoda)	sea slug suckers	particulate suction feeding
Burrowed worms	burrowed worm suckers	particulate suction feeding
Bottom surface worms	benthic worm suckers	particulate suction feeding
Tube worms	tube worm biters/suckers	biting/particulate suction
Sea stars (Asteroidea)	sea star biters	biting at sea stars
Burrowed sea urchins (Echinoidea)	burrowed urchin crushers	crushing urchin
Bottom surface sea urchins (Echinoidea)	benthic urchin crushers	crushing urchin
Brittle stars (Ophiuroidea)	brittle star suckers	particulate suction feeding
Sea cucumbers (Holothuroidea)	sea cucumber biters	biting at sea cucumbers
Burrowed bivalves: siphons (Bivalvia)	burrowed bivalve biters	biting at bivalve siphons
Bottom surface bivalves (Bivalvia)	benthic bivalve crushers	crushing whole shells
Shrimp (Malacostraca)	shrimp ambush hunters	sprinter, jumping at prey
	shrimp pursuit hunters	cruiser, pursuing prey
Walking lobsters (Malacostraca)	crab suckers	particulate suction feeding
Bottom surface crabs (Malacostraca)	crab suckers	particulate suction feeding
Burrowing crabs (Malacostraca)	burrowed crab suckers	particulate suction feeding
Cephalopods (Cephalopoda)	ambush hunters	sprinter, jumping at prey
	pursuit hunters	cruiser, pursuing prey
Bottom surface fish	ambush hunters	sprinter, jumping at prey
	pursuit hunters	cruiser, pursuing prey
Burrowed fish	burrowed fish suckers	particulate suction feeding
Pelagic fish	ambush hunters	sprinter, jumping at prey
	pursuit hunters	cruiser, pursuing prey

A table was made that showed the optimal value as demanded by each variable for each food category to construct a food specialist for every food-type. In those cases where the values of several food specialists were equal multiple specialists were combined into one. The advantage of food specialists over food categories is that they are directly comparable to real fish. By correlating the feeding variables measured on real fish with those of the theoretical food specialists, we can quantify the degree of specialisation.

The demands food makes on the fish also depend on prey size. However prey size was not quantified in any way. Instead, when generating optimal variable values for each food specialist, a feeding strategy was connected to a food category, depending on its general relative size to the fish. Plankton was defined as too small to be eaten as particular items, and a choice was made to have plankton ‘make the demand’ of filter feeding on fish morphology. Other items were defined as being too big or too hard to be swallowed whole and those were deemed as demanding biting, crushing or scraping strategies from the fish. See the food specialist table (table 7) for a complete overview. As all food categories also occur in size ranges small enough to be eaten by all fish larger than 100 mm (the lower limit for fish size, see section 2.6.3 in the materials and methods for details) no lower size limit for fish mouth size was demanded from specialists.

Food specialist variable scores:

This section summarises the morphological variables and their food specialist scores. The latter is expressed in arbitrary units and indicates what consequences a low or high score have for fish feeding. For each food-type, table 7 presents the optimal value for each morphological variable.

- **Orbita length:** relates to light conditions and prey size.
  Score 1-3. Higher values are demanded for prey that is better camouflaged, smaller and/or (partly) burrowed.
- **Total barbel length:** indicates focus on benthic prey.
  Score 1-3. Demands depend on prey (in)visibility and mainly on its connection to the substrate. Prey demanding long barbels may be burrowed and/or inconspicuous and/or mixed with indigestible material.
- **Body depth:**
  Score 1-5. Low values are demanded from fish that swim fast and/or long and therefore benefit from a smaller frontal profile in the water to reduce drag or their threatening silhouette. High values are beneficial for fish that must depend on stability and manoeuvrability to reach slow but less accessible prey.
- **Oral gape area/frontal body area:**
  Score 1-5. A relatively large mouth reduces water flow resistance. This means that fish that rely on speed to catch their prey (pursuit hunters for example) need relatively large mouths, while fish that specialize on particulate suction feeding and/or less accessible prey benefit from a small tubular mouth (cf. pipette-feeding in pipefish).
- **Aspect ratio caudal fin:**
  Score 1-5. Fish with high slender caudal fins (high scores) suffer less drag, but can generate less thrust when accelerating; hence they are excellent cruisers. Fish with low broad caudal fins (low scores) are powerful accelerators but suffer too much from drag to maintain a high speed for longer periods of time.
- **Caudal peduncle depth:**
  Score 1-5. A high caudal peduncle enhances acceleration. A low or narrow peduncle helps to minimize drag on the fish and is required for cruising fish.

- **Oral gape axis:**
  Score 1-3:
  1. Supra-terminal or superior orientation demanded.
  2. Terminal orientation demanded.
  3. Sub-terminal or inferior orientation demanded.

  Fish that forage on food items on or in the bottom benefit most from a sub-terminal or inferior orientation (3). Fish that hunt fast prey moving freely in the water column benefit most from a terminal orientation (2). Fish that burrow and ambush prey that swim overhead likely show oral gapes pointing upwards (1).
- **Protrusion length:** particulate feeding vs. biting.
  Score 1-5. Suction and/or particulate feeders demand high values to suck in their food faster and more directed. Fish requiring large mouth openings, but that do not rely on fast suction, such as plankton townet feeders, also benefit from protrusion because it increases their mouth size. Jaws of biting fish are weakened by protrusion however and this means biters require low values.
- **Lower jaw length:** biting/scraping.
  Score 1-5. Fish that need to maximize biting or scraping force require a shorter jaw. Fish that need to have large gapes because they need to process large volumes of prey or water and/or because they need to minimize swimming resistance need a long jaw.
- **Hyoid length:** biting/scraping vs. suction
  Score 1-5. Low values are demanded when fish specialize in biting or scraping and consequently need a mouth opening of small amplitude. A long hyoid means increased suction power.
- **Opercular sealing flap width:** relates to suction feeding.
  Score 1-5. A broad flap enables greater head expansion prior to mouth and opercular opening, which means a greater build-up of negative pressure. Suction feeders need high values to increase suction volume and power. Fish that do not require strong suction require low scores to minimize energy cost.
- **Volume capacity operculum:** relates to suction feeding.
  Score 1-5**.** An elongate operculum, i.e. a high value, allows for greater suction volumes. In ambush hunters a high value is demanded because fast and voluminous suction plays a relatively big role in covering the predator-prey distance. Fish that do not require strong suction require low scores to minimize energy cost.
- **Branchial outlet:** suitability for pursuit hunting.
  Score 1-3. Fish that need to pass large volumes of water through their mouths and branchial outlets, for example pursuit hunters, require a large opening.
- **Gill arch resistance:** fast suction vs. filter feeding.
  Score 1-5. This is a trade-off between fast swimming and filter feeding. Fast swimmers need low values, while filter feeders need high values. This means a filter feeder cannot combine its feeding mode with high swimming speeds.

- **Maxillar and mandibular teeth types:** relates to prey mastication.
  Score 1-5 based on the shape of the contact area with the prey:
  1. Pointed
  2. Pointed-chisel
  3. Chisel
  4. Chisel-plate
  5. Plate

  Fish feeding on whole, soft prey items require pointed teeth; biting or scraping fish demand chisel-like teeth and fish foraging on hard, impenetrable prey (bivalves) require plate-like crushing teeth.
- **Oral gape diameter:**
  Score 1-5. Particulate feeders require small gape sizes to increase suction speed and precision. Large gapes are required by fish that need to specialize in cruising and/or by fish that need to pass large volumes through their mouth.
- **Gill raker length:** large prey vs. filter feeding.
- Score 1-5. Only food types that need to be filtered out of the water, for instance plankton, demand long rakers. Short rakers are demanded for large, fast prey because they reduce resistance.
- **Gill interraker distance:** large prey vs. filter feeding.
  Score 1-5. Gill interraker distances need only be small in filter feeders. For hunters of large, fast prey longer interraker distances are beneficial as they decrease resistance.
- **Postlingual organ width:** large prey vs. filter feeding.
  Score 1-3. Large prey as well as struggling prey requires a high value. Combined the highest value is required.
- **Type of pharyngeal teeth:** relates to prey mastication.
  Score 1-5 based on contact area with prey:
  1. Pointed
  2. Pointed-chisel
  3. Chisel
  4. Chisel-plate
  5. Plate

  Fish feeding on whole, soft prey items require pointed teeth; biting or scraping fish demand chisel-like teeth and fish foraging on hard, impenetrable prey require plate-like crushing teeth. Pointed teeth increase transport capacity.
- **Gut length:** fish vs. detritus
  Score 1-5. Gut length is dependant on the amount of indigestible materials in the prey. High protein content means that shorter guts are adequate. Fish that forage on other fish show shortest gut lengths while fish that feed on plant material or detritus have the longest. Crustaceans and echinoderms were scored in between.

The following variables were not used in the food specialist creation step and subsequently not in any other analyses either; therefore no specialist values were generated. However, measurements required for these variables were performed (unless otherwise specified) and the results are found on the appendix CD.

- **Nostril distance:** no connection was made between the nostril distance and the olfactory sensitivity of the fish. The sense of smell in fish seemed dependant on other important factors such as nasal cavity size (De Groot 1971).
- **Maxillar/mandibular teeth density:** due to limited time and the difficulty of interpreting the true function of this variable, teeth density was not used to base conclusions on.
- **Pharyngeal teeth density:** due to limited time and the difficulty of interpreting the true function of this variable, pharyngeal teeth density was not used to base conclusions on.
- **Pharyngeal teeth inclination:** because the measurements showed too little variance, pharyngeal teeth inclination was not used to base conclusions on.
- **Stomach size:** because the measurements showed too little variance, stomach size was not used to base conclusions on.
- **Pyloric ceca size:** measurements failed for this variable. In most fish the pyloric ceca were unrecognisably damaged.

2.5 Measurements

Main sampling:

Fish were sampled between: 22/08 - 14/09/2005 with RV “Tridens” during the Beam Trawl Survey (BTS), by two 8m. beam trawls rigged with a cod-end mesh of 40mm and towed at 2 m/s or 30 minutes over the sea bed. A total of 71 hauls were made during the sampling period throughout the North Sea between 51oN and 58oN. A sampling chart depicting the sampling stations is given in figure 2.

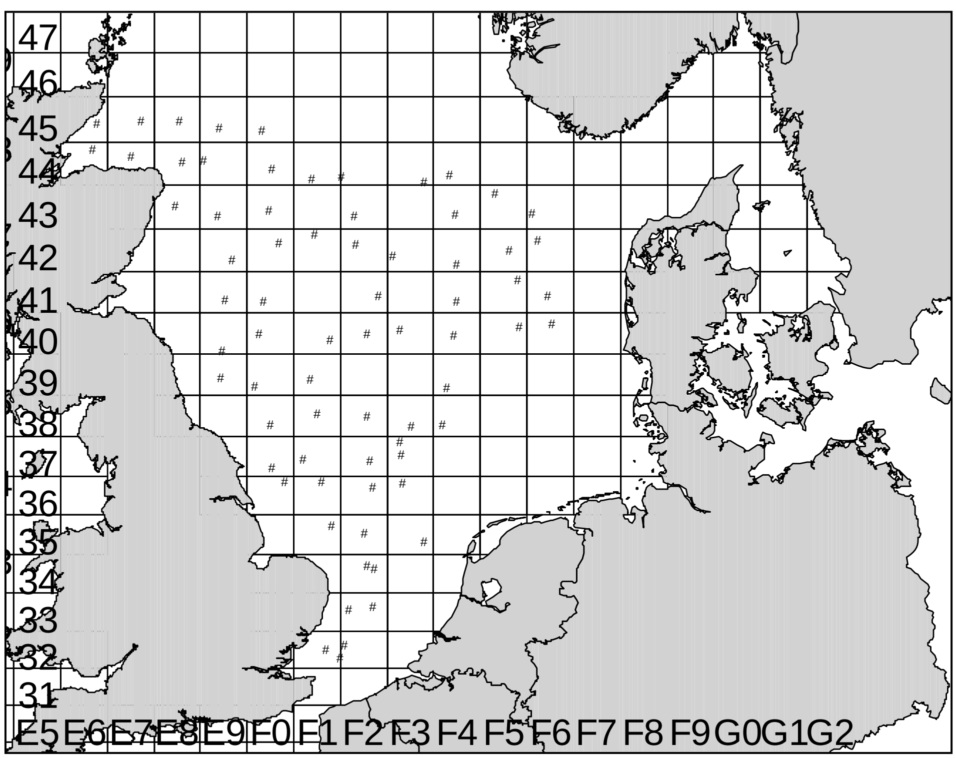


Figure 2. Chart of North Sea indicating all sampling stations of the main sampling.

After each haul fish were selected, measured (total length and fresh weight), tagged, wrapped in plastic and frozen individually.

Secondary sampling:

Not all species were sufficiently sampled in the main sampling period. RV “Isis” caught the following species to supplement: Brill (*Scophthalmus rhombus*), Flounder (*Platichthys flesus*), Scaldfish (*Arnoglossus laterna*), Solenette (*Buglossidium luteum*) and Turbot (*Scophthalmus maximus*). The ‘Isis’ sampled from 01/10 till 31/10 in 2005 during the Demersal Fish Survey (DFS) using two 6m. beam-shrimp trawl rigged with a 20mm cod-end mesh size at a haul duration of 15 min. Sampling area was the coastal waters of the Netherlands and Germany.

Sampling selection:

An essential characteristic of the method is that fish size was not taken into account when comparing among individuals. Fish lengths were used only to determine *relative* values for most measurements (often given as a ratio to standard length). One size-related condition was that measured fish were old enough to show only isometric growth. Fish that were too young would still have shown allometric growth and this would have made relative measurements incomparable. Fish in their allometric growth phase have reached their adult and final body form with all its options and limitations for foraging.
The first selective criterion that was used to sample only adult fishes was that individuals should be at least large enough as to have reached 25% of their maximum length (pers. comm. FA Sibbing), smaller specimens were also taken however. For maximum length ‘fishbase’ was consulted (“Fishbase,” 2005) (with the exception of Long rough dab, *Hippoglossoides platessoides*, for this species the ‘Atlas of North Sea fish’ was used (Knijn et al. 1993).

The selected species comprised the 30 most abundant North Sea fish species, based on their estimated total biomass between 1977 - 1986 (Daan et al. 1990). The species list was altered during the sampling period: some target species were caught too few or not at all and removed from the list. While other species that were not targeted but were caught a lot were added.

Per species the goal was to collect:

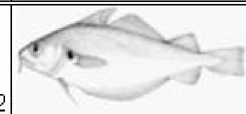
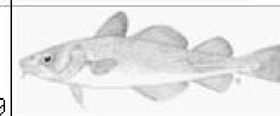
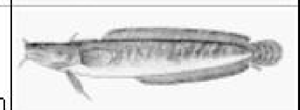
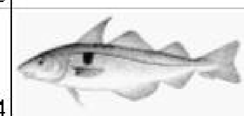
- 5 specimens, 10-25% of maximum length.
- 15 specimens, 25-50% of maximum length.
- 5 specimens, 50-100% of maximum length.

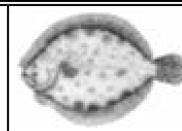
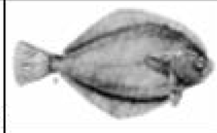
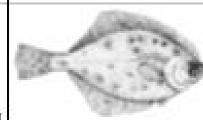
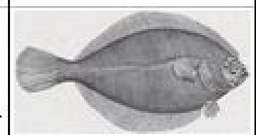
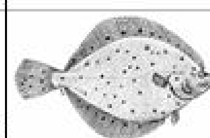
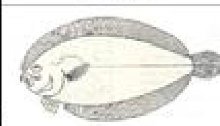
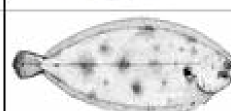
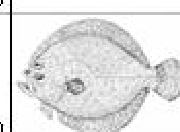
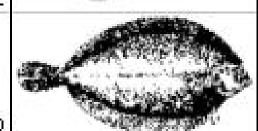
For several species this was difficult however and for some even impossible.

Fish selection for measurements:

Because of the limitations imposed by the fishing method and time available for measurements a selection was made on the final samples to be analysed. The focus is on inter-specific variation, not on intra-specific variation. This means that the number of species is more important than the number of animals per species. Accordingly only 3-5 individuals per species were measured, making it possible to maintain a large number of species. Analysis was limited to two orders: the Gadiformes and the Pleuronectiformes. A total list of all species used in the experiment is given in table 2.

Table 2. List of sampled species.

Species (eng.)	Species (lat.)	Species (nl)	% Biomass	Picture
Bib	*Trisopterus luscus*	Steenbolk	0,2	
Cod	*Gadus morhua*	Kabeljauw	10,9	
Four-bearded rockling	*Rhinonemus cimbrius*	4-Dradige meun	0,0	
Haddock	*Melanogrammus aeglefinus*	Schelvis	13,4	
Hake	*Merluccius merluccius*	Heek	0,2	
Ling	*Molva molva*	Leng	0,5	
Norway pout	*Trisopterus esmarkii*	Kever	12,2	
Poor cod	*Trisopterus minutus*	Dwergbolk	1,5	
Whiting	*Merlangius merlangus*	Wijting	10,5	

Species (eng.)	Species (lat.)	Species (nl)	% Biomass	Picture
Brill	*Scophthalmus rhombus*	Griet	0,1	
Dab	*Limanda limanda*	Schar	34,3	
Flounder	*Platichthys flesus*	Bot	0,0	
Long rough dab	*Hippoglossoides platessoides*	Lange schar	3,7	
Lemon sole	*Microstomus kitt*	Tongschar	2,9	
Megrim	*Lepidorhombus whiffiagonis*	Scharretong	0,4	
Plaice	*Pleuronectes platessa*	Schol	7,9	
Scaldfish	*Arnoglossus laterna*	Schurftvis	0,0	
Sole	*Solea solea*	Tong	0,9	
Solenette	*Buglossidium luteum*	Dwergtong	0,0	
Turbot	*Scophthalmus maximus*	Tarbot	0,2	
Witch	*Glyptocephalus cynoglossus*	Witje	0,2	

Measurements:

The morphological measurements from which the trophic variables were derived are listed in Table 3. The morphological measurements themselves are included separately on the appendix disc.

For several variables the required measurements failed, although specialist values were generated for them. The following variables were dropped at this stage:

- **% White muscle fibre in tail:** in most fish no red muscle could be detected. In some fish deviating colours were seen, but no clear boundaries between different types of tissue could be found.
- **Gill raker profile:** gill raker profiles were not present in the measured fish. All rakers were smooth (excepting brushes of teeth, those will be explained later). Therefore this variable does not discriminate among species in the current study.
- **Pointed anterior pharyngeal teeth:** all fish measured had pointed anterior pharyngeal teeth. Therefore this variable is not of any use in this research.

Morphological measurements not only had to be compared among Pleuronectiformes and Gadiformes but also between these orders. This caused difficulties, as flatfish are asymmetrical. As this research is based on *functional* morphology, variables were interpreted strictly functional. For example: when looking at ‘Oral gape orientation’, from an anatomical point of view, an ‘inferior’ orientation would mean that the flatfish has a mouth pointing to its anatomical ventral side. Lying on its side, this would mean either pointing to the left or right. An inferior orientation of the mouth is interpreted as pointing towards the bottom in this study however, as it gives the fish easier access to prey on or in the bottom. In the case of the natural position of the fish, this means to the lateral side of the flatfish. Diagrams and photos describing the measurements are given in figures 3 and 4.

Table 3. List of measurements. All measurements including the unit in which they were measured as well as a description of how the measurement was performed. Numbers that refer to elements of figure 3 are given in brackets.

Measurement	Unit	Description
PHOTO fish	-	fins spread with pins, photo made with ruler
PHOTO oral gape orientation	-	cone in the mouth
max. orbita length	mm	see fig. 3 (7)
max. distance between nose in- and outflow openings	mm	see fig. 4H
body depth	mm	(flatfish: thickness) see fig. 3 & 4A
body width	mm	(flatfish: broadness) see fig. 3 & 4B
total length	mm	from tip of nose to most caudal tip of tail
standard length	mm	from tip of nose to visual start of caudal fin rays
oral gape height	mm	see fig. 3 (17)
oral gape width	mm	see fig. 3 (18)
min. caudal peduncle depth	mm	see fig. 3 (6)
head length	mm	see fig. 3 (11)
single opercular sealing flap width	mm	see fig. 4C
postorbital length	mm	see fig. 3 (25)
operculum height	mm	see fig. 3 (19)
max branchial outlet	mm	see fig. 4D
protrusion dorsal part premaxilla	mm	(flatfish: ocular side) see fig. 3 (26)
protrusion ventral part premaxilla	mm	(flatfish: ocular side) see fig. 4E
lower jaw length	mm	(flatfish: ocular side) see fig. 3 (13)
pharyngeal gape width	mm	calibrated staves are inserted into the mouth and pharynx
barbels #	#	total number of barbels on the head
average barbel length	mm	average length of all barbels on the head
hyoid length	mm	see fig. 3 (12)
mouthfloor width between 2nd gill arches	mm	see fig. 3 (24)
maxillar teeth type	1-5	Classified as 1:point, 3:chisel, 5:plate
mandibular teeth type	1-5	Classified as 1:point, 3:chisel, 5:plate
maxillar teeth #	#	maxillar teeth on one half of upper jaw
mandibular teeth #	#	mandibular teeth on one half of lower jaw
maxillar teeth # rows	#	maxillar teeth rows on one half of upper jaw
mandibular teeth # rows	#	mandibular teeth rows on one half of lower jaw
tooth plates #	#	all tooth plates in the mouth and pharynx
pointed anterior pharyngeal teeth	0-1	absent or present
upper, largest plate pharyngeal tooth type	1-5	Classified as 1:point, 3:chisel, 5:plate
upper, largest plate pharyngeal tooth inclination	1-3	Classified as 1:rostral, 2:straight, 3:caudal
upper, largest plate pharyngeal tooth plate length	mm	length measured rostra-caudally
upper, largest plate pharyngeal tooth plate width	mm	width measured media-laterally
upper, largest plate pharyngeal teeth #	#	pharyngeal teeth fused on the plate
lower plate pharyngeal tooth type	1-5	Classified as 1:point, 3:chisel, 5:plate
lower plate pharyngeal tooth inclination	1-3	Classified as 1:rostral, 2:straight, 3:caudal
stomach description	1-3	Classified as 1:thicker gut to 3:balloon
gut length	mm	end of stomach to anus
paeloric ceca #	#	pyloric appendages below the stomach
paeloric ceca length	mm	average length of one appendage
PHOTO musclecoupe	-	cross-section at 2/3 SL from the nosetip
PHOTO gill raker	-	through a binocular microscope
gill raker length	mm	average length of one raker
gill arch length over 5 rakers	mm	from tip of raker 1 to tip of raker 5
gill raker profile	1-5	Classified as 1:smooth to 5: jagged

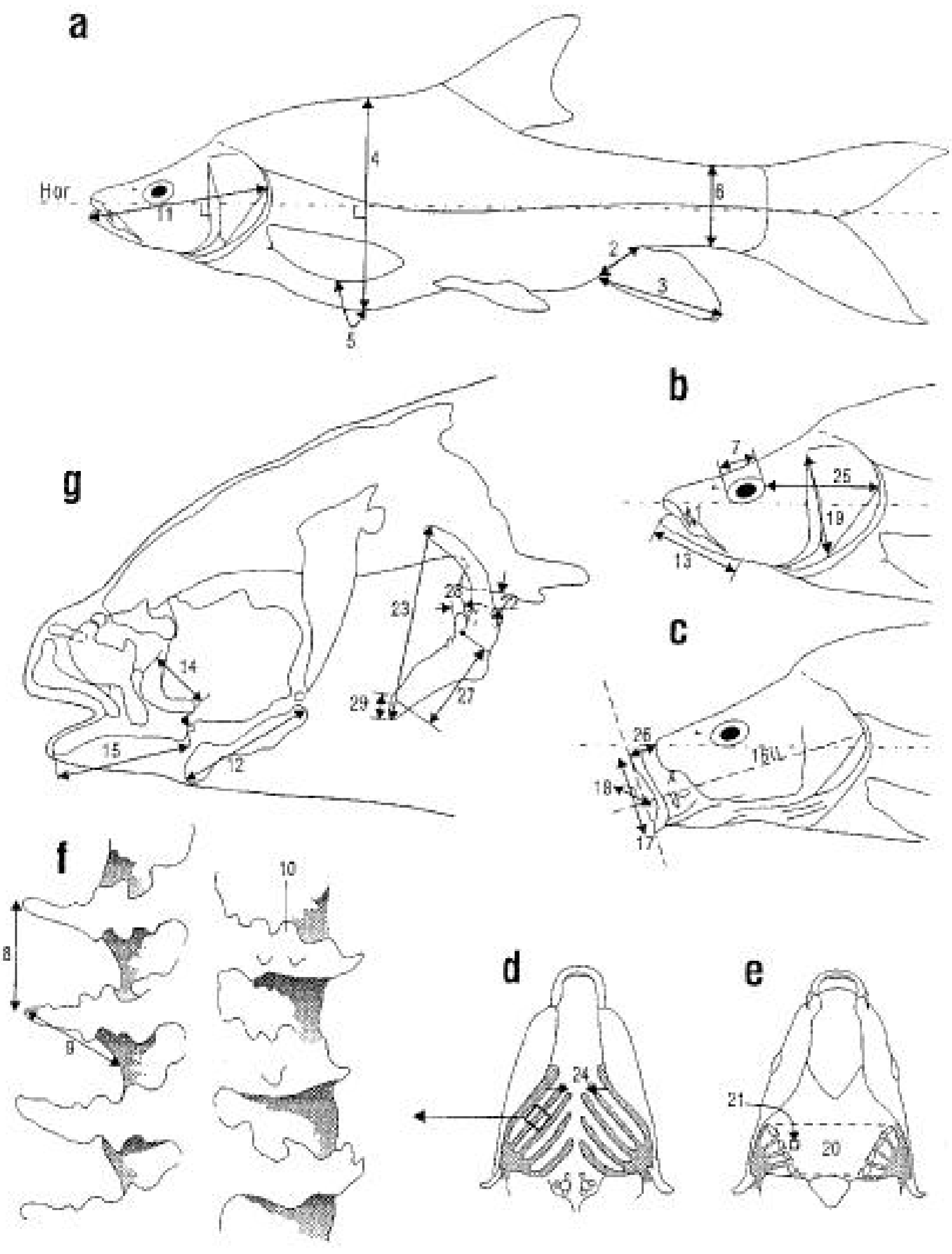


Figure 3. Fish morphometrics. Most morphological measurements are shown. For a description of the numbers refer to table 3. After Sibbing and Nagelkerke (2001).

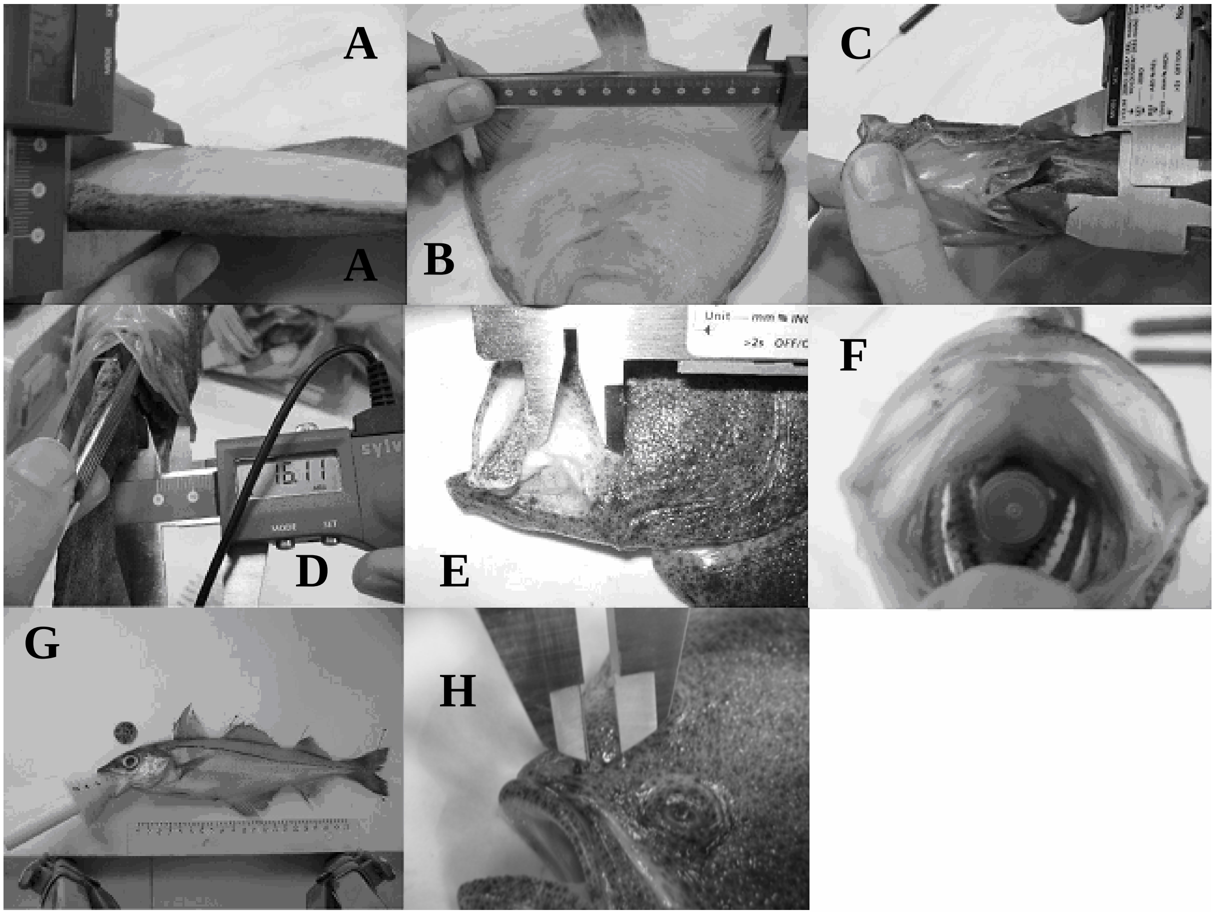


Figure 4. Photographs showing several measurements in detail. A. 'Body depth' measurement in flatfish; **B. '**Body width' measurement in flatfish; **C.** 'Opercular sealing flap width' measurement in flatfish; **D. '**Branchial outlet' measurement in flatfish; **E.** 'Ventral premaxillar protrusion' measurement in flatfish; **F. '**Pharyngeal gape width' measurement; **G.** 'Gape orientation' measurement; **H.** 'Distance between nose in- and outflow openings' measurement.

Measurements given in millimetres were measured with a digital calliper gauge connected to a pc via a foot pedal, except for *gut length*, *standard length* and *total length*, which were measured with a ruler and *pharyngeal gape width* that was measured using plastic rods with a calibrated diameter. The ruler and the rods had an accuracy of 1 mm. Some measurements were derived from a digital photograph made from a tri-pod. To analyse those pictures (see table 4) the graphic software "ImageJ" was used.
The photo used to measure *Oral gape axis* was made while a plastic cone with a cylindrical handle to indicate the axis was inserted into the maximally opened mouth of the fish (see figure 4g). Gill raker length, gill interraker distance and gill raker profile were measured under a binocular microscope also using the digital calliper gauge.

Some measurements failed due to damage done to the fish. If there were no other sample fish to replace the damaged specimen, the lost measurement was replaced by an artificially created one, which will be explained in the section on 'data repair'. The heads of some fish were damaged badly during otolith extraction on board the research vessel 'Tridens'. Otoliths were removed for other purposes than the current study. Some fish were cut open for sex-determination also for purposes other than this research. Another recurring problem was the damage done to the intestine. This often made it difficult or even impossible to measure *gut length*.

After all measurements were done, they were transformed into variables. Table 4 shows the calculations made to obtain a value for each variable.

Variables were given as relative (i.e. dimensionless) values by dividing most measurements by the standard length because this made comparing between fish of different size possible. These were noted as ‘SL-ratio’ in table 4. A few have different but still relative values. In some cases this was not appropriate and the exceptions are explained below:

- **Maxillar/mandibular teeth type, Gill raker profile, Pointed anterior pharyngeal teeth, Pharyngeal tooth type, Pharyngeal teeth inclination, Stomach size:** these variables have absolute values. However they are not strictly quantitative but divided in classes. The values are size-independent and comparable so no alterations were made.
- **Maxillar/mandibular teeth density:** a variable that gives an absolute value as well, although this is quantitative. This is also size-independent, so it was not changed.
- **Oral gape axis:** this variable was measured in “ImageJ” as the angle of the cone in the mouth with the body axis of the fish and the unit used was degrees. This unit was not deemed appropriate because the measuring inaccuracy was larger than 1°. For this reason the unit was transformed into classes of 32° based on the most extreme values measured:
    1. 48° to 80° = superior
    2. 16° to 48° = supra-terminal
    3. –16° to 16° = terminal
    4. –48° to -16° = sub-terminal
    5. –48° to –80° = inferior

Table 4. Variables indicating trophic morphology and their calculations, and final units. SL-ratio: the variable is expressed as a ratio of Standard Length of the fish, i.e. SL/measurement.

Parameter	calculation	unit
Orbita length	max. orbita length/standard length	SL-ratio
Nostril distance	max. distance between nose in- and outflow openings/standard length	SL-ratio
Barbel length	(barbels # * average barbel length)/standard length	SL-ratio
Body depth	body depth/standard length	SL-ratio
Oral gape area/frontal body area	oral gape width + height averaged = diameter --> oral gape area, body depth + body width averaged = diameter --> frontal body area --> (gape area/body area)/standard length	SL-ratio
% White muscle fibre in tail	Total muscle area outlined and calculated in ImageJ, surface area red muscle outlined and calculated in ImageJ --> 100% - %red	%
Aspect ratio caudal fin	(caudal fin height measured in ImageJ)^2/surface area caudal fin outlined and calculated in ImageJ	ratio
Caudal peduncle depth	min. caudal peduncle depth/standard length	SL-ratio
Oral gape axis	gape axis (degrees) measured in ImageJ	class: 1-5
Protrusion length	protrusion dorsal part premaxilla/standard length	SL-ratio
Lower jaw length	lower jaw length/standard length	SL-ratio
Hyoid length	hyoid length/standard length	SL-ratio
Opercular sealing flap width	single opercular sealing flap width/standard length	SL-ratio
Volume capacity operculum	postorbital length/operculum height	ratio
Branchial outlet	max. branchial outlet/standard length	SL-ratio
Gill arch resistance	gill raker length/(gill arch length over 5 rakers/4)	ratio
Maxillar/mandibular teeth type	maxillar/mandibular teeth type	class: 1-5
Maxillar/mandibular teeth density	maxillar/mandibular teeth # * # rows	-
Oral gape diameter	(oral gape width + height averaged)/standard length	SL-ratio
Gill raker length	gill raker length/standard length	SL-ratio
Gill inter-raker distance	(gill arch length over 5 rakers/4)/standard length	SL-ratio
Gill raker profile	gill raker profile	class: 1-5
Postlingual organ width	mouthfloor width between 2nd gill arches/standard length	SL-ratio
Pointed anterior pharyngeal teeth	pointed anterior pharyngeal teeth	class: 0-1
Upper pharyngeal teeth type	upper, largest plate pharyngeal teeth type	class: 1-5
Lower pharyngeal teeth type	lower plate pharyngeal teeth type	class: 1-5
Pharyngeal teeth density	upper, largest plate pharyngeal teeth #/(upper, largest plate pharyngeal teeth plate length * upper, largest plate pharyngeal teeth plate width)	ratio
Upper pharyngeal teeth inclination	upper, largest plate pharyngeal teeth inclination	class: 1-3
Lower pharyngeal teeth inclination	lower plate pharyngeal teeth inclination	class: 1-3
Gut length	gut length/standard length	SL-ratio
Stomach size	stomach description	class: 1-3
Pyloric ceca size	(paeloric ceca # * paeloric ceca length)/standard length	SL-ratio

2.6 Analysis

Data repair:

After measurements were done and variable values were calculated the resulting dataset was checked on ‘outlying’ values using “SAS”. Outliers were defined as deviating from the average by more than 4 standard deviation units. Outliers were considered erroneous values (likely due to measuring errors) and removed from the dataset.
Failed measurements were another cause for gaps in the data. To fill these gaps the following formula was used:

$$V = \mu + \sigma R$$

Where μ is the mean and σ is the standard deviation of the comparable measurements and R is a random number drawn from a normal distribution with mean=0 and standard deviation = 1.
For comparable measurements other individuals of the incomplete species and individuals from species with similar values were used if possible. If all values for one species for a variable were missing, they were replaced using all other Gadiformes in the case of Gadiformes or all other Pleuronectiformes in the case of Pleuronectiformes.
Another point was the absence of values for the variable ‘gill interraker distance’ for sole (*Solea solea*) and solenette (*Buglossidium luteum*). This was caused by the fact that soles and solenettes have no gill rakers and therefore the distance between them could not be measured. To solve this problem, the highest interraker distance variable value shown among all other fish (in this case the turbot) was doubled, and this value was used for sole and solenette.

The PCA method:

This study produced results in tables containing multiple individuals and 22 variables. While the tables are very informative, they fail to clearly identify large patterns in the crowded data. To visualize patterns in the results multivariate analysis was used.
The type of analysis used was principal component analysis (PCA). The function and limitations of the PCA can be found in ‘Principal Component Analysis’ by I.T. Jolliffe (2002).
PCA’s were performed on:

- Food categories (individuals are food types; variables are food properties)
- Food specialists (individuals are specialist fish; variables are variables)
- Measurements (individuals are measured fish; variables are variables)
- Fish diet (individuals are species; variables are food categories)

For the PCA’s the program “Canoco 4.5” was used. Values were standardized and centred prior to analysis (value - average/std.deviation).

<u>Correlation:</u>
A correlation matrix was made to compare the food specialists and the measured fish with each other and so indicate the predictive power of the morphological measurements. Variable values were averaged per species. For correlation the program "NTSYSpc2" was used. Significance of correlations was calculated using $p<0.05$ and DF = 20.

2.7 Stomach contents

<u>Fish diet:</u>

Actual fish diet was obtained from stomach content analyses in literature. Table 5 lists literature used for each fish species.

Table 5. Stomach content data literature. The literature used to obtain diet information for all species. Author and year of publication is given for each article used. Full records can be found in the reference section. Due to small sample sizes, areas of sampling outside the North Sea, young age of the fish sampled and low level of detail in stomach content determination, some sources were less reliable than others and those are marked grey.

Species	Author	Publ. year
Trisopterus luscus	Armstrong	1982
	Steven	1930
Scophthalmus rhombus	Braber	1973
	Wyche	1986
	Cabral	2002
	Piet	1998
	Wetsteijn	1981
Gadus morhua	Pearcy	1979
	Mattson	1990
	Armstrong	1982
Limanda limanda	Wyche	1986
	Piet	1998
	Steven	1930
	Arntz	1971
	Braber	1973
Rhinonemus cimbrius	Mattson	1981
Platichthys flesus	De Vlas	1979
	Piet	1998
	Doornbos	1984
Melanogrammus aeglefinus	Albert	1995
	Mattson	1992
Merluccius merluccius	Cabral	2002
Microstomus kitt	Rae	1965
	Steven	1930
	Piet	1998
Molva molva	Daan	pers.comm.

Species	Author	Publ. year
Hippoglossoides platessoides	Ntiba	1993
Lepidorhombus whiffiagonis	Morte	1999
Trisopterus esmarkii	Albert	1995
	Mattson	1981
Pleuronectes platessa	De Vlas	1979
	Wyche	1986
	Braber	1973
	Doornbos	1984
	Piet	1998
	Rijnsdorp	2001
Trisopterus minutus	Albert	1995
	Armstrong	1982
	Mattson	1990
Arnoglossus laterna	Cabral	2002
	Piet	1998
Solea solea	Braber	1973
	Rijnsdorp	2001
	Piet	1998
Buglossidium luteum	Cabral	2002
	Piet	1998
Scophthalmus maximus	Braber	1973
	Piet	1998
	Wetsteijn	1981
Merlangius merlangus	Hislop	1991
Glyptocephalus cynoglossus	Mattson	1981

Weight percentages as indicators for relative importance of food categories were preferred. However in the case of brill (*Scophthalmus rhombus*) and turbot (*Scophthalmus maximus*) 'frequency of occurrence' data was used. For ling (*Molva molva*), only very little information was available in the form of non-analysed stomach content results of 7 individuals obtained through personal communication with N. Daan.

Data from literature was always interpreted to best ability in order to subdivide into classes defined in the food categories. If determination in literature was not to a sufficient level, the weight percentage given was added to all food categories that fit the determination.

<u>Correlation with morphological predictions:</u>

Using "SAS" stomach contents were correlated with the morphological predictions in two different ways:
(a) DIET SPECTRA
The diet spectra approach correlates the predicted diets per species with the actual diets per species. Also for each species the 'relative fit' of the prediction for that species is calculated: looking at the predicted diet of a species, the lowest correlation with an actual diet is set at 0% and the highest correlation with an actual diet is set at 100%. The correlation of the predicted diet of a species with the actual diet of the same species is somewhere on this scale, this percentage is called relative fit.
(b) FOOD PARTITIONING
The food partitioning approach correlates the predicted relative importance of a food category among all species with the relative importance of food categories found in the actual diet. For this correlation a relative fit was calculated as well.

<u>Predictions and Stomach content cluster analysis:</u>

A cluster analysis was performed on the data of both the morphological predictions and the stomach contents. The morphological predictions cluster analysis was done on the correlation table of specialists versus measurements, with species averaged before correlation and without standardization. For the stomach content data the cluster analysis was done using arcsine transformed weight percentages.
The program "DGGEStat" was used for the analyses and the program "Treeview" to transform them into rootless trees.

3 RESULTS:

3.1 Food categories & properties

All food categories used in the research are listed in table 6. The functional physical properties are listed for each food-type.

Table 6. Food categories and properties. All food categories used are listed in the first column with their functional properties in the following columns. Explanations of properties are as follows: Burst escape: 1 = slow, 3 = fast; Position in water column: 1 = Burrowed, 2 = Attached to substrate, 3 = Benthic free moving, 4 = Pelagic free moving; Strength, Compliance, Fibrousness, Toughness: 1 = low, 5 = high.

Food Type (Class)	Burst-escape	Elongate shape	Position in water column	Protein/ Carbohydrate	Indigestible	Strength	Compliance	Fibrousness	Toughness
	scale: 1-3	0 = absent 1 = present	scale: 1-4	0 = protein 1 = carboh.	0 = absent 1 = present	scale: 1-5	scale: 1-5	scale: 1-5	scale: 1-5
Phytoplankton	1	0	4	1	1	3	3	2	3
Sessile microalgae	1	0	2	1	0	3	3	2	3
Macrophytes/thallous weeds/macroalgae	1	0	2	1	0	3	3	3	3
Detritus	1	0	3	1	0	3	3	3	3
Microzoos	2	0	4	0	0	3	3	3	3
Benthic fish-eggs	1	0	2	0	0	2	3	2	2
Sponges (Porifera)	1	0	2	0	1	3	3	3	3
Sea anemones (Anthozoa)	1	0	2	0	0	3	4	4	4
Corals (Anthozoa)	1	0	2	0	1	3	4	3	3
Hydropolyps (incl. moss animals)	1	0	2	0	0	3	4	3	3
Sea squirts: adult (Ascidiacea)	1	0	2	0	0	3	4	4	4
Jellyfish (Scyphozoa)	1	0	4	0	0	1	5	1	2
Sea snails: with shell (Gastropoda)	1	0	3	0	1	5	1	2	3
Sea slugs: without shell (Gastropoda)	1	0	3	0	0	2	4	4	3
Burrowed worms	2	1	1	0	0	2	4	3	3
Bottom surface worms	2	1	3	0	0	2	4	3	3
Tube worms	2	1	1	0	1	2	4	3	3
Sea stars (Asteroidea)	1	0	3	0	1	3	3	3	3
Burrowed sea urchins (Echinoidea)	1	0	1	0	1	4	2	2	3
Bottom surface sea urchins (Echinoidea)	1	0	3	0	1	4	2	2	3
Brittle stars (Ophiuroidea)	1	0	3	0	1	3	2	3	3
Sea cucumbers (Holothuroidea)	1	1	3	0	0	3	4	4	4
Burrowed bivalves: siphons (Bivalvia)	1	0	1	0	1	4	1	2	2
Bottom surface bivalves (Bivalvia)	1	0	2	0	1	4	1	2	2
Shrimp (Malacostraca)	3	1	3	0	1	3	3	3	3
Walking lobsters (Malacostraca)	3	1	3	0	1	4	2	3	3
Bottom surface crabs (Malacostraca)	2	0	3	0	1	4	2	3	3
Burrowing crabs (Malacostraca)	2	0	1	0	1	4	2	3	3
Cephalopods (Cephalopoda)	3	1	4	0	1	3	4	4	4
Bottom surface fish	3	1	3	0	0	3	4	5	4
Burrowed fish	3	1	1	0	0	3	4	5	4
Pelagic fish	3	1	4	0	0	3	4	5	4

This table was used as input for a PCA on the food categories (Fig. 5).

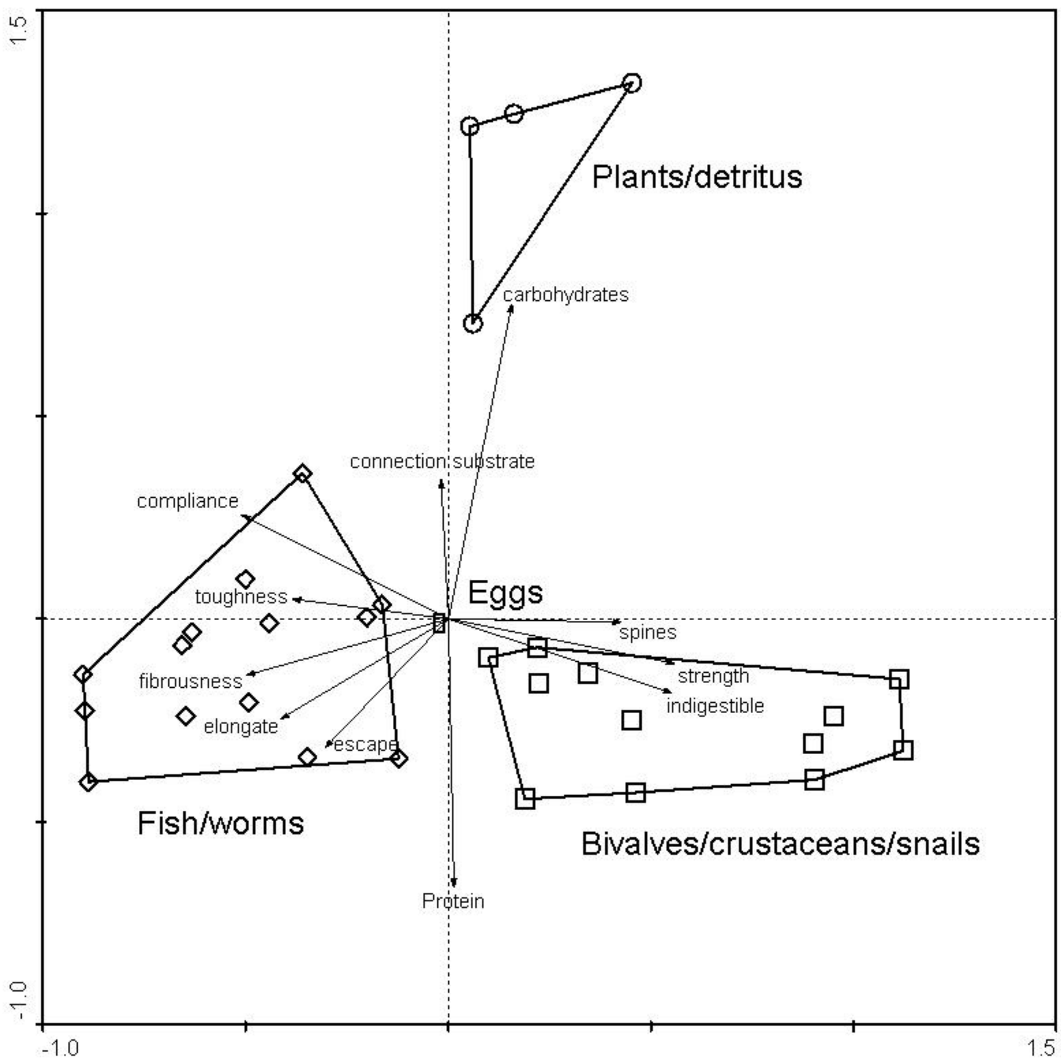


Figure 5. PCA graph of food categories and properties. Total variance visualized: 33,8% axis 1; 21,7% axis 2. Points represent food categories; arrows represent physical/chemical food properties. Lines drawn around symbols of the same type reflect arbitrarily chosen functional groups.

Different groups of food types were identified as deviating from each other due to the effect of the variables (physical properties): *Plants/detritus*, containing mostly carbohydrates; *Bivalves/crustaceans/snails*, including all animals with lots of indigestible body parts such as shells; *Fish/worms*, animals that are long, fast and/or compliant; *Eggs*, fish eggs.

3.2 Food specialists

The food specialist values are given in table 7. The table shows a value for each food specialist for each variable. A clarification on the range of values for each variable can be found in table 7. The food specialist values from this table were used as input for a PCA (Fig. 6).

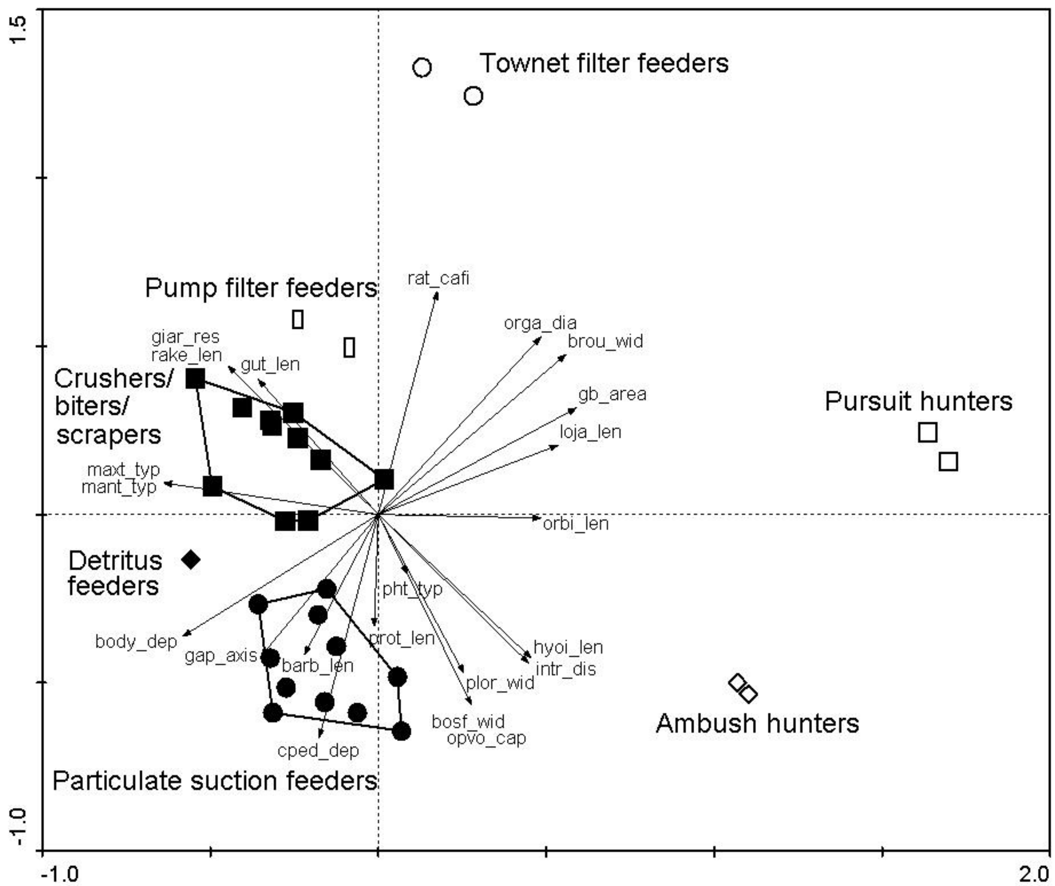
This PCA graph is different from the food category graph in figure 5 in that it compares food specialists with morphological variables, instead of food categories with physical properties. Seven classes were defined in the graph: *Townet filter feeders*; *Pump filter feeders*; *Crushers/biters/scrapers*, containing all specialists that use (oral) jaws to forage on mostly sessile animals and plants; *Pursuit hunters*; *Detritus feeders*; *Ambush hunters*; *Particulate suction feeders*, comprised of all specialists that use aimed suction to ingest prey items such as crabs and sea slugs.
Whereas table 7 gives absolute variable values needed for the specialists, the PCA graph in figure 6 shows how variables must be combined or which variables must be maximized or minimized to excel at foraging on a desired food type. The graph shows that *particulate suction feeders* - that mostly feed on benthic or burrowed organisms - benefit from a combination of a deep caudal peduncle (greater manoeuvrability), an inferior gape axis (improved access to benthic or burrowed food), a deep body (greater manoeuvrability) and long barbels (improved sensing of benthic or burrowed food). Variables that hinder this group of specialists are: a high caudal fin aspect ratio (a 'cruiser-tail', decreasing manoeuvrability), a large oral gape (decreasing suction speed), a large branchial outlet (making for costly suction) and a long lower jaw (decreasing suction speed).
Crushers/biters/scrapers are mostly defined by the teeth type variables, which need to be high, but they also score high on 'gut length', because these food types often contain many indigestible parts. Variables that maximize suction capability such as the width of the opercular sealing flap and the volume capacity of the operculum need to be held low.
Pump filter feeders and *townet filter feeders* are separated by 'swimming style' variables: townet filter feeders need a high caudal fin aspect ratio and large oral gape, as well as low bodies and a narrow caudal peduncle.
Pursuit hunters and *ambush hunters* both need large eyes and mouths, combined with low teeth type values that indicate pointed teeth. They are separated mostly by caudal peduncle depth and caudal fin aspect ratio, which need to be high and low respectively in ambush hunters and the opposite in pursuit hunters.
Detritus feeders have high scores on 'body depth', 'gut length', 'barbel length' and 'oral gape axis', combined with low values for mouth size and branchial outlet width.

Table 7. Food specialists. Theoretical variable values are shown for each food specialist. Morphological variables are listed in the first column and food specialists in the upper row. For further explanation of the specialist names, variables and values, see section 2.5.1 in the materials and methods.

Parameter	phyto-townet	phyto-pump	sessile-algae	macro-phyte	detritus	zoo-townet	zoo-pump	egg	polyp	sea-squirt	jellyfish	sea-snail	sea slug	burrowed-worm	benthic-worm	tube-worm
Orbita length	1	1	2	2	1	2	2	2	2	1	1	1	2	1	2	1
Barbel length	1	1	1	1	3	1	1	2	1	1	1	1	1	3	2	2
Body depth	2	3	4	4	3	2	3	4	4	4	3	4	5	4	4	4
Gape-/frontal body area	5	3	2	2	2	5	3	2	2	2	2	3	3	2	2	2
% White muscle	1	3	3	3	3	1	3	3	3	3	3	3	3	4	4	4
Aspect ratio caudal fin	5	3	3	3	3	5	3	3	3	3	3	3	3	2	2	2
Caudal peduncle depth	1	3	3	3	3	1	3	3	3	3	3	3	3	4	4	4
Oral gape axis	2	2	3	2	3	2	2	3	2	2	2	3	3	3	3	3
Protrusion length	4	3	3	1	5	4	3	5	3	1	2	3	4	4	4	4
Lower jaw length	5	3	2	1	2	5	3	2	2	1	2	2	2	2	2	2
Hyoid length	3	3	2	1	4	3	3	4	2	1	2	4	4	4	4	4
Volume capacity operculum	1	4	1	1	4	1	4	4	1	1	1	4	4	4	4	4
Opercular sealing flap width	1	4	1	1	4	1	4	4	1	1	1	4	4	4	4	4
Maxillar teeth type	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3
Mandibular teeth type	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3
Branchial outlet	3	2	1	1	1	3	2	1	1	1	1	1	1	1	1	1
Gill arch resistance	5	5	4	3	4	5	5	4	3	3	3	3	3	3	3	3
Oral gape diameter	5	4	3	3	1	5	4	1	3	3	3	1	1	2	2	2
Gill raker length	5	5	4	3	4	5	5	4	3	3	3	3	3	3	3	3
Gill inter-raker distance	1	1	2	3	2	1	1	2	3	3	3	3	3	3	3	3
Gill raker profile	5	5	4	3	4	5	5	4	3	3	3	3	3	3	3	3
Postlingual organ width	1	1	1	3	1	1	1	1	2	2	2	2	2	2	2	2
Pointed anterior pharyngeal teeth	1	1	1	3	1	1	1	1	2	2	2	1	3	3	3	3
Pharyngeal teeth type	1	1	1	1	1	1	1	1	1	1	1	5	1	1	1	1
Gut length	4	4	4	4	5	2	2	1	3	3	3	3	1	2	1	2

Parameter	sea star	burrowed-urchin	benthic-urchin	brittle-star	sea-cucumbe	burrowed-bivalve	benthic-bivalve	shrimp-pursuit	shrimp-ambush	crab	burrowed-crab	pursuit-hunter	ambush-hunter	anemone/coral/sponge	burrowed-fish
Orbita length	1	1	1	1	1	2	2	3	3	2	1	3	2	1	1
Barbel length	1	2	1	1	1	2	1	1	1	1	2	1	1	1	2
Body depth	3	4	3	4	3	4	3	1	2	4	4	1	2	4	4
Gape-/frontal body area	3	3	3	3	2	2	3	5	4	3	3	5	4	2	3
% White muscle	3	3	3	3	3	4	3	1	5	4	4	1	5	3	4
Aspect ratio caudal fin	3	3	3	3	3	2	3	5	1	2	2	5	1	3	2
Caudal peduncle depth	3	3	3	3	3	4	3	1	5	4	4	1	5	3	4
Oral gape axis	3	3	3	3	3	3	3	2	2	3	3	2	2	2	2
Protrusion length	3	5	3	3	3	5	3	3	4	4	5	3	3	2	5
Lower jaw length	4	4	4	2	2	2	3	5	4	4	4	5	5	2	3
Hyoid length	3	3	3	4	3	2	3	5	5	4	4	5	5	2	5
Volume capacity operculum	1	1	1	4	3	4	1	4	5	4	4	4	5	1	5
Opercular sealing flap width	1	1	1	4	3	4	1	4	5	4	4	4	5	1	5
Maxillar teeth type	2	3	3	3	3	3	5	1	1	3	3	1	1	3	3
Mandibular teeth type	2	3	3	3	3	3	5	1	1	3	3	1	1	3	3
Branchial outlet	1	1	1	1	1	1	1	3	2	1	1	3	2	1	1
Gill arch resistance	3	3	3	3	3	3	3	1	2	3	3	1	2	3	3
Oral gape diameter	2	2	2	2	3	2	1	5	4	2	2	5	4	3	2
Gill raker length	3	3	3	3	3	3	3	1	2	3	3	1	2	3	3
Gill inter-raker distance	3	3	3	3	3	3	3	5	4	3	3	5	4	3	3
Gill raker profile	3	3	3	3	3	3	3	1	2	3	3	1	2	3	3
Postlingual organ width	2	2	2	2	2	2	2	2	2	3	3	3	3	2	3
Pointed anterior pharyngeal teeth	2	2	2	2	3	2	1	2	2	1	1	3	3	2	3
Pharyngeal teeth type	3	1	1	3	1	1	5	3	3	3	3	1	1	1	1
Gut length	3	3	3	3	3	3	3	2	2	2	2	1	1	3	1

A PCA was performed on the results in table 7 (fig. 6).



Label	Parameter	Label	Parameter
orbi_len	Orbita length	bosf_wid	Opercular sealing flap width
barb_len	Barbel length	mant_typ	Mandibular teeth type
body_dep	Body depth	maxt_typ	Maxillar teeth type
gb_area	Gape-/frontal body area	brou_wid	Branchial outlet
rat_cafi	Aspect ratio caudal fin	giar_res	Gill arch resistance
cped_dep	Caudal peduncle depth	orga_dia	Oral gape diameter
gap_axis	Oral gape axis	rake_len	Gill raker length
prot_len	Protrusion length	intr_dis	Gill inter-raker distance
loja_len	Lower jaw length	plor_wid	Postlingual organ width
hyoi_len	Hyoid length	pht_typ	Pharyngeal teeth type
opvo_cap	Volume capacity operculum	gut_len	Gut length

Figure 6. PCA graph of food specialists. Total variance visualized: 32,5% axis 1; 24,5% axis 2. The dots represent the individual food specialists; arbitrarily chosen functional groups are defined by symbol type. The arrows depict the variables; their label codes are explained in the figure legend.

3.3 Trophic morphology of the North Sea fishes

The calculated morphological variables of each individual fish of all species were used as input for a PCA. This PCA reveals several groups of fish with similar trophic morphology (Fig. 7):

Each of the groups was formed by a shared combination of scores on morphological variables:

- *Soles* (sole *Solea solea*, solenette *Buglossidium luteum*) distance themselves by having a relatively high ‘barbel length’ (in the case of soles many barbels), long guts, and large interraker distances (soles have no gill rakers, for further explanation see the materials and methods). Naturally because they have no gill rakers they score low on ‘gill raker length’ and ‘gill arch resistance’. They generally score opposite values in comparison with *large-mouthed flatfish*.
- *Small-mouthed flatfish* (dab *Limanda limanda,* witch *Glyptocephalus cynoglossus*, lemon sole *Microstomus kitt*, plaice *Pleuronectes platessa,* flounder *Platichthys flesus*) are positioned in the bottom right part of the graph and are separated mostly by having high scores in teeth type, meaning they possess molar, biting or scraping teeth, both oral and/or pharyngeal. Small-mouthed flatfish also have low body depths (body depth being measured as ‘thickness’ in flatfish) and a relatively small mouth.
- *Large-mouthed flatfish* (scaldfish *Arnoglossus laterna*, long rough dab *Hippoglossoides platessoides,* brill *Scophthalmus rhombus*, turbot *Scophthalmus maximus,* megrim *Lepidorhombus whiffiagonis*) share the characteristics of having short guts, short barbels (they had none), a relatively fine gill sieve (high scores on ‘gill arch resistance’ and ‘gill raker length’ and low scores on ‘gill interraker distance’), long lower jaws and hyoid arches, large branchial outlets and large protrusions, among others.

- *Other Gadiformes* (cod *Gadus morhua*, bib *Trisopterus luscus*, poor cod *Trisopterus minutus*, norway pout *Trisopterus esmarkii*, hake *Merluccius merluccius*, whiting *Merlangius merlangus*) appear on the left side of the graph just as *large-mouthed flatfish*. This means they show similar morphology when considering the variables pointing either left or right, i.e. 'gut length', eye size, gape openings and axis etc. Yet they are dissimilar when looking at gill raker properties, barbel length, gape size relative to frontal body area and others that point mostly up or down. The gadiform fish possess barbels, have relatively large mouths compared to their frontal body area and have a wider gill raker mesh.
- *Ling/Rockling/Haddock* (ling *Molva molva*, four-bearded rockling *Rhinonemus cimbrius*, haddock *Melanogrammus aeglefinus*) are found at slight distance from *other Gadiformes*. They are relatively close to the centre of the graph, indicating that they show non-extreme values for most variables. They form the middle group between *other Gadiformes* and *soles*, meaning they have longer barbels and guts than *other Gadiformes* but have larger mouths, longer hyoid arches and lower jaws, larger eyes and larger branchial outlets, to name a few, than *soles*.

Some variable arrows are shorter than others. Those shorter arrows indicate variables that have less effect on the spread of the different groups in this PCA diagram. 'Volume capacity operculum' and 'postlingual organ width' are both rather unimportant in this graph and 'aspect ratio caudal fin' has almost no influence.

3.4 Measurements versus food specialists

Another PCA was done on the combined data of food specialists and morphological measurements. In figure 8 two graphs are displayed, both graphs result from the same PCA and have equally scaled axes. Specialists are compared to measurements.

- *Soles* show some resemblance to specialists in macrophytes and animals like anemones, corals, sea squirts, sponges etc. Sea star and burrowed worm specialists are in the same graph quarter as well.
- *Small-mouthed flatfish* are similar to some suction-feeding specialists (brittle star, tube worm, detritus) but also to many biters, crushers and scrapers (sea cucumber, sea urchins, sea snail, bivalves, sessile algae), which are drawn to the lower right part of the graph together with the *small-mouthed flatfish* largely due to the teeth type variable.

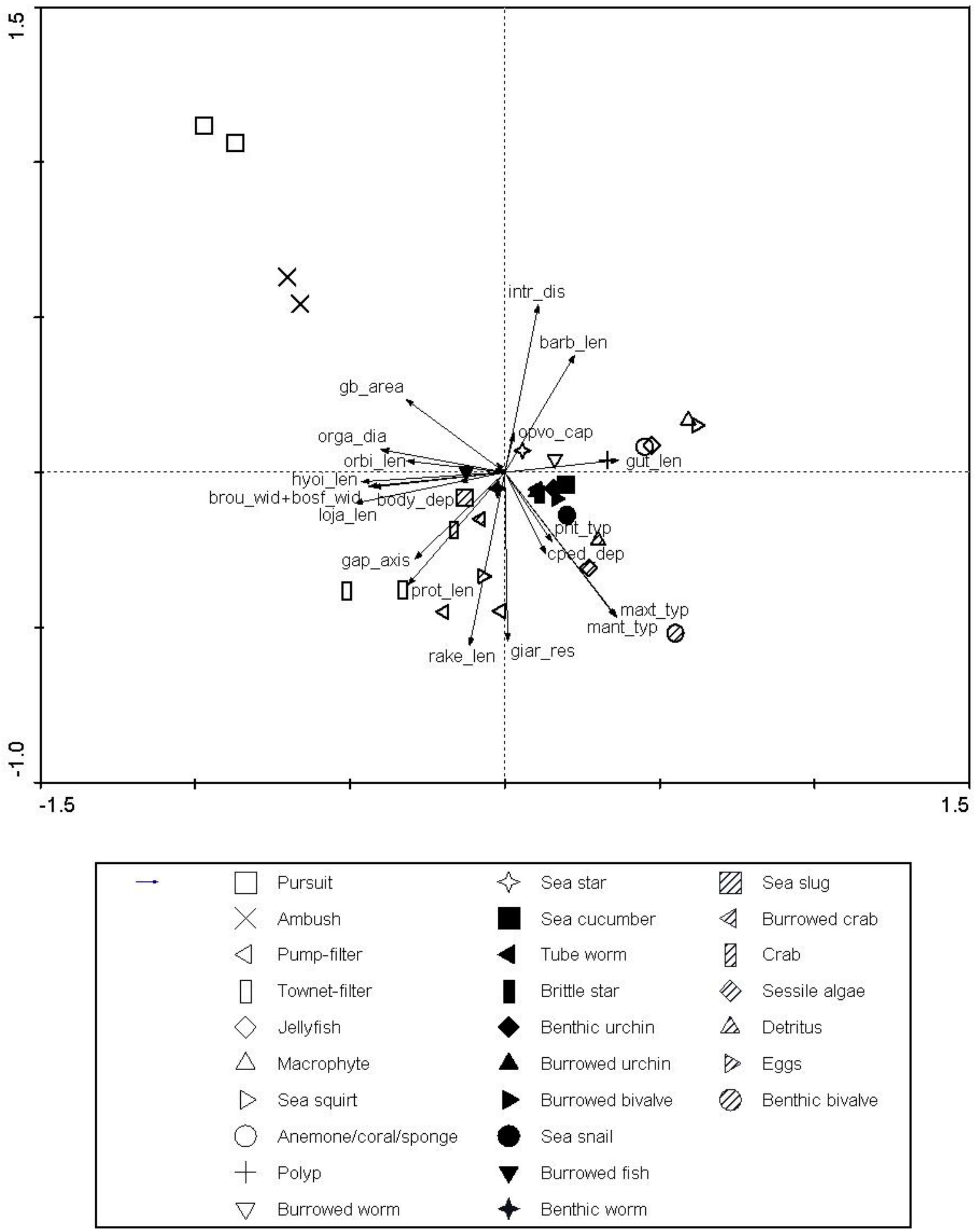


Figure 8. PCA of morphological measurements & food specialists combined. Total variance visualized: 28.8% axis 1; 16.3% axis 2. The arrows depict the morphological variables.

Figure 8a. Food specialists. Symbols represent food specialists. For an explanation see legend.

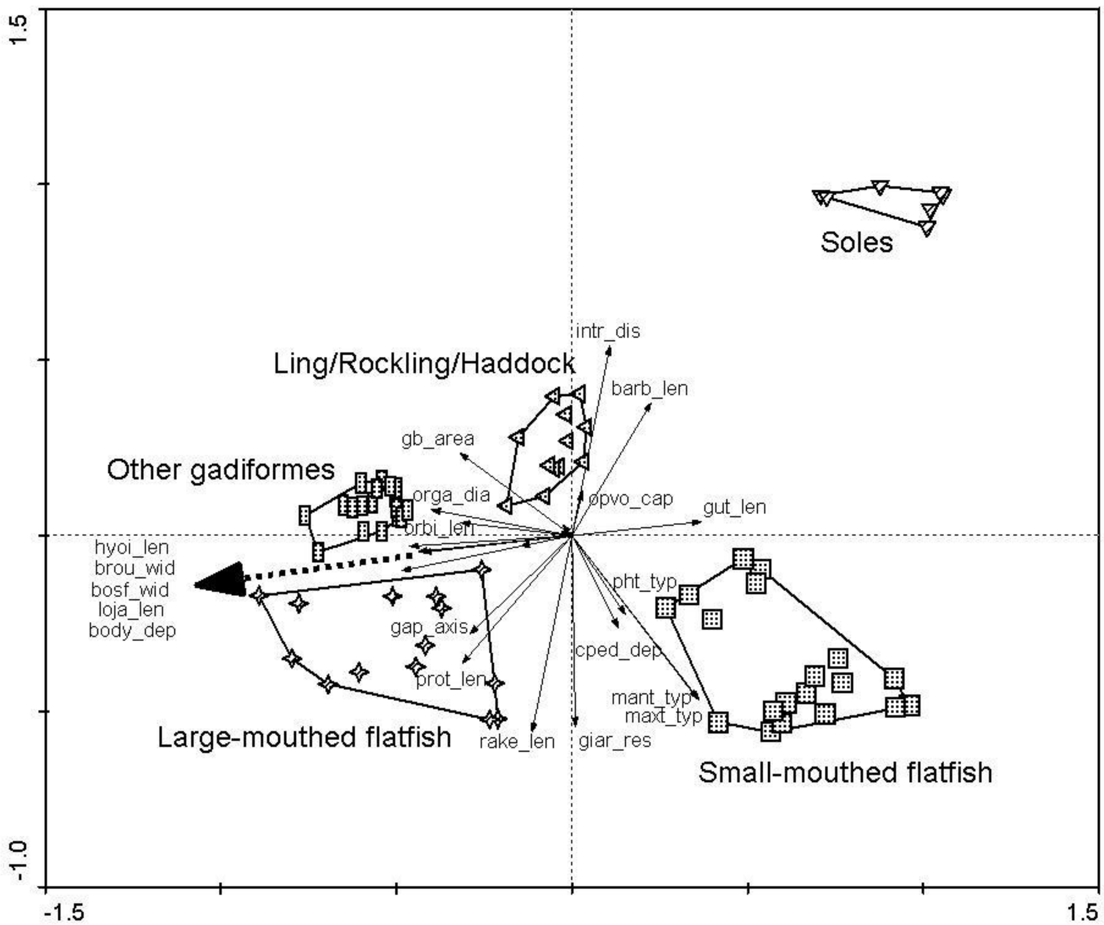


Figure 8b. Morphological measurements. 5 main groups are recognized equal to those in figure 7 (fish are arbitrarily, functionally grouped *post hoc)* and indicated by symbol, a surrounding line and label.

- *Large-mouthed flatfish* appear in the same area as the townet- and pump filter feeders as well as some particulate suction feeders (benthic worm, sea slug, burrowed crab, eggs and crab). *Large-mouthed flatfish* and suction feeders share high values for 'hyoid length', 'branchial outlet width' and 'opercular sealing flap width'. Both the *large-mouthed flatfish* and the filter feeders have long gill rakers and short gill interraker distances, yet the flatfish distinguish themselves by showing higher scores on the abovementioned variables.
- *Ling/Rockling/Haddock* are closest to sea star, burrowed worm, burrowed fish and benthic worm eaters. They are however for the greatest part present in the upper left quarter of the graph, therefore appearing similar to ambush- and to a lesser extent to pursuit hunters as well.
- *Other Gadiformes* are positioned close to most particulate suction feeding specialists such as the burrowed fish and crab, sea slug, benthic worm and fish-egg eaters. They are also placed in the upper left quarter of the graph and in this way approach ambush hunters and pursuit hunters.

Table 8. Correlations of measurements with food specialists. Measured fish species are correlated with predicted food specialists. Italics indicate highest and lowest values per row; highest and lowest values per column are underlined; significant values (p<0.05; r>0.44) are in bold script.

fish species	phyto-townet	phyto-pump	sessile-algae	macro-phyte	detritus	zoo-townet	zoo-pump	egg	polyp	sea-squirt	jellyfish	sea-snail	sea slug	burrowed-worm	benthic-worm	tube-worm
Bib	-0.275	*-0.377*	0.013	0.164	-0.322	-0.143	-0.183	0.088	0.153	-0.050	-0.280	-0.050	***0.537***	-0.068	0.222	-0.021
Brill	0.035	0.139	-0.050	***-0.580***	0.165	0.061	0.185	*0.370*	-0.399	**-0.461**	-0.334	-0.106	0.112	0.074	0.169	0.199
Cod	-0.150	-0.172	-0.330	-0.162	-0.202	-0.151	-0.178	-0.107	-0.264	-0.274	*-0.377*	0.011	0.235	0.047	0.100	0.114
Dab	0.013	0.278	***0.486***	0.314	0.251	0.010	0.287	0.295	0.415	0.404	**0.471**	0.026	0.015	0.068	0.102	0.112
Rockling	0.095	0.032	-0.350	-0.163	-0.077	0.075	-0.001	-0.132	*-0.369*	-0.122	-0.287	0.135	0.108	-0.034	-0.145	-0.090
Flounder	-0.177	0.006	0.018	0.294	0.029	-0.270	-0.132	-0.158	0.186	0.320	0.402	**0.575**	-0.135	0.019	-0.065	0.087
Haddock	-0.171	-0.078	0.350	*0.376*	0.021	-0.198	-0.118	-0.015	0.316	0.198	-0.042	0.139	0.278	-0.083	-0.006	-0.076
Hake	0.204	-0.086	-0.260	*-0.342*	-0.279	0.222	-0.069	-0.188	-0.161	-0.334	-0.196	-0.311	-0.170	-0.058	-0.073	-0.044
Ling	-0.208	-0.201	-0.101	-0.242	0.063	-0.310	-0.361	-0.165	*-0.399*	-0.233	-0.302	0.208	0.015	0.239	0.095	0.263
Long rough dab	**0.488**	**0.479**	-0.123	-0.269	-0.083	**0.532**	***0.555***	-0.003	-0.257	-0.263	-0.167	-0.378	-0.275	-0.325	-0.263	-0.318
Lemon sole	0.046	0.315	**0.551**	**0.465**	0.325	-0.058	0.169	0.074	**0.463**	**0.563**	***0.609***	0.120	-0.128	0.083	-0.025	0.113
Megrim	0.284	0.165	-0.031	-0.407	-0.279	***0.447***	0.416	0.100	-0.269	-0.344	-0.300	-0.397	-0.110	-0.178	0.041	-0.172
Norway pout	0.187	-0.086	-0.018	-0.431	-0.107	0.330	0.125	0.302	-0.272	**-0.525**	***-0.681***	-0.097	***0.446***	-0.214	0.040	-0.205
Poor cod	0.178	-0.026	0.123	-0.062	-0.131	0.255	0.086	0.059	-0.050	-0.199	*-0.425*	-0.084	0.319	-0.314	-0.126	-0.328
Plaice	-0.116	0.023	0.128	0.367	0.093	-0.234	-0.154	-0.195	0.271	0.351	**0.462**	**0.541**	-0.207	-0.053	-0.163	-0.005
Scaldfish	0.243	0.351	0.207	*-0.339*	0.226	0.323	**0.484**	***0.501***	-0.222	-0.249	-0.235	-0.088	0.141	-0.083	0.054	-0.038
Sole	-0.193	-0.179	0.025	0.343	0.345	-0.334	*-0.399*	-0.215	0.250	0.435	***0.446***	0.025	-0.351	0.372	-0.036	0.153
Solenette	-0.258	-0.252	-0.247	*0.347*	0.105	-0.342	*-0.386*	-0.267	0.135	0.347	0.324	0.080	-0.144	0.185	-0.057	0.046
Turbot	-0.010	-0.014	-0.291	-0.271	-0.228	0.028	0.044	-0.039	-0.261	-0.307	-0.146	-0.301	-0.072	0.015	0.110	0.133
Whiting	0.102	-0.115	-0.036	-0.276	-0.326	0.194	0.016	-0.038	-0.165	-0.308	*-0.400*	-0.197	0.162	-0.143	0.026	-0.114
Witch	-0.087	-0.064	0.106	0.304	-0.021	0.004	0.075	0.123	**0.503**	0.251	0.369	-0.100	0.025	0.020	0.162	0.005

fish species	sea star	burrowed-urchin	benthic-urchin	brittle-star	sea-cucumbe	burrowed-bivalve	benthic-bivalve	shrimp-pursuit	shrimp-ambush	crab	burrowed-crab	pursuit-hunter	ambush-hunter	burrowed-fish	anemone/coral/sponge
Bib	-0.005	-0.018	-0.115	0.026	-0.164	0.056	-0.246	0.171	0.095	0.319	0.008	0.269	0.140	0.035	-0.051
Brill	0.131	0.037	0.046	-0.064	0.068	0.008	-0.357	-0.030	0.188	0.023	0.090	-0.022	0.215	0.149	-0.392
Cod	-0.039	-0.080	-0.144	0.130	-0.085	-0.101	-0.366	0.266	0.260	0.285	0.211	0.333	*0.384*	0.257	-0.227
Dab	-0.093	0.092	0.185	-0.023	0.251	0.228	0.399	***-0.668***	**-0.508**	-0.084	-0.103	***-0.659***	**-0.530**	-0.088	0.406
Rockling	-0.072	-0.099	-0.140	0.198	-0.232	-0.103	-0.163	0.218	0.133	0.016	0.108	*0.220*	0.185	0.171	-0.248
Flounder	0.074	-0.049	0.116	**0.443**	0.271	0.035	***0.744***	-0.396	-0.305	0.311	0.304	***-0.468***	-0.359	0.056	0.326
Haddock	0.029	-0.015	-0.057	0.213	-0.016	0.139	-0.050	-0.008	-0.071	0.099	-0.179	-0.039	-0.167	*-0.247*	0.182
Hake	0.074	0.208	0.032	-0.266	-0.133	-0.239	-0.268	0.262	0.217	0.069	0.217	0.309	*0.318*	0.188	-0.160
Ling	0.239	0.171	0.213	*0.367*	0.251	0.058	-0.055	0.095	0.139	0.266	0.332	0.055	0.186	-0.001	-0.231
Long rough dab	-0.099	-0.329	-0.234	***-0.445***	-0.302	-0.291	**-0.442**	0.245	0.295	-0.286	-0.309	0.272	0.329	-0.042	-0.283
Lemon sole	-0.137	0.130	0.277	0.126	0.418	0.279	**0.582**	**-0.694**	**-0.596**	-0.163	-0.138	***-0.725***	**-0.646**	-0.211	**0.532**
Megrim	-0.053	-0.228	-0.129	*-0.421*	-0.229	-0.277	-0.274	0.307	0.332	-0.125	-0.244	0.313	0.334	-0.161	-0.347
Norway pout	-0.032	0.038	-0.135	-0.081	**-0.466**	-0.091	-0.224	0.339	0.215	0.048	-0.127	0.333	0.105	-0.070	**-0.538**
Poor cod	-0.046	-0.118	-0.163	-0.018	-0.309	-0.112	-0.265	*0.413*	0.170	-0.114	-0.384	0.392	0.054	-0.298	-0.267
Plaice	0.151	0.025	0.204	0.395	0.279	0.051	***0.773***	-0.399	-0.347	0.253	0.231	***-0.484***	-0.431	-0.055	0.370
Scaldfish	0.009	-0.091	-0.061	-0.120	-0.045	0.014	-0.192	-0.130	-0.068	-0.174	-0.196	-0.138	-0.117	-0.101	-0.298
Sole	0.067	0.221	0.063	-0.002	0.110	0.197	0.051	-0.021	-0.100	-0.392	-0.043	-0.087	-0.138	-0.065	0.397
Solenette	-0.048	-0.081	-0.092	0.097	0.125	0.063	-0.083	0.218	0.020	-0.240	-0.078	0.220	0.060	0.065	0.262
Turbot	0.137	0.001	0.057	-0.277	0.028	-0.108	*-0.426*	0.032	0.269	0.250	0.283	0.171	**0.496**	0.319	-0.205
Whiting	0.050	0.010	-0.033	-0.105	-0.210	-0.223	-0.280	0.352	0.265	0.087	-0.065	*0.361*	0.275	-0.092	-0.250
Witch	*-0.406*	0.069	-0.026	-0.224	-0.051	0.264	**0.593**	-0.350	-0.266	0.073	0.022	-0.318	-0.345	0.145	0.282

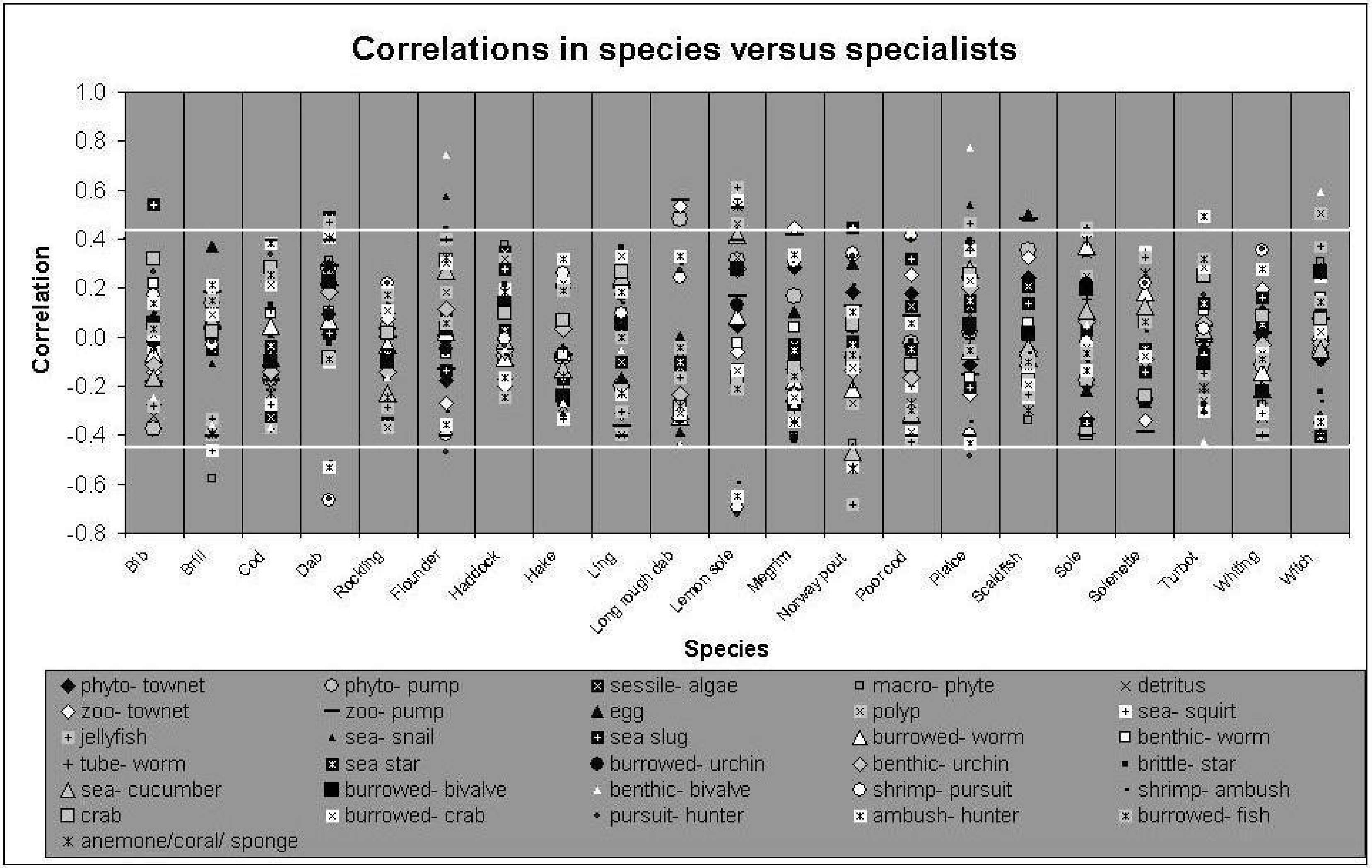


Figure 9. Correlations of measurements with food specialists. Fish species correlated with food specialists. Different specialists are represented by symbols explained in the figure legend. Significant results are shown above the upper horizontal white line and below the lower horizontal white line.

The morphologies of the food specialists and the North Sea species were also compared directly by calculating the correlations between the measured morphology of the sample fish and the theoretical values of the food specialists (Table 8, Fig. 9). We found that:

- *Soles* show positive correlations with jellyfish, macrophytes, sea squirts and anemones/corals/sponges, although these are low. So they seem specialized on attached tough prey.
- *Small-mouthed flatfish* show high correlations with biting/crushing/scraping specialists. When looking at sessile algae, macrophytes, polyps, sea squirts, jellyfish, sea snails, benthic bivalves and anemones/corals/sponges they correlate, often significantly, positively with *small-mouthed flatfish*, at the same time this group of flatfish show (also many significant) negative correlations with specialists in shrimp and fish hunting. So they seem biters/scrapers.
- *Large-mouthed flatfish* correlate mostly negatively with biters/crushers/scrapers, but show largely positive correlations with specialists in zooplankton, eggs, sea stars, shrimp, pursuit hunting and ambush hunting. So they seem hunters.
- *Ling/Rockling/Haddock* correlate above average with brittle star, shrimp, crab and pursuit hunting specialists, and below average with specialists in plankton, eggs, jellyfish and benthic bivalves. None of the species in this group shows extreme correlations, neither negative nor positive, and none are significant. So they seem generalists.
- *Other Gadiformes* show positive correlations with sea slug, shrimp, crab, pursuit hunting and ambush hunting specialists. With other specialists they show varied correlations, most of which are average, although many correlate negatively with most biters/crushers/scrapers. So they seem hunters.

Biting/crushing/scraping specialists can be seen in the upper range in *small-mouthed flatfish*, but in the lower ranges of Gadiformes and *large-mouthed flatfish* - while ambush hunting, pursuit hunting and shrimp specialists appear high in Gadiformes and *large-mouthed flatfish* and low in *small-mouthed flatfish*. Correlations are distributed quite evenly for all species. Species can be compared among one another: flounder and plaice show great similarity in predicted diet choice, as well as norway pout and poor cod.

3.5 Actual diets

Fish diet observed from the literature on stomach analyses is summarized in figure 10.

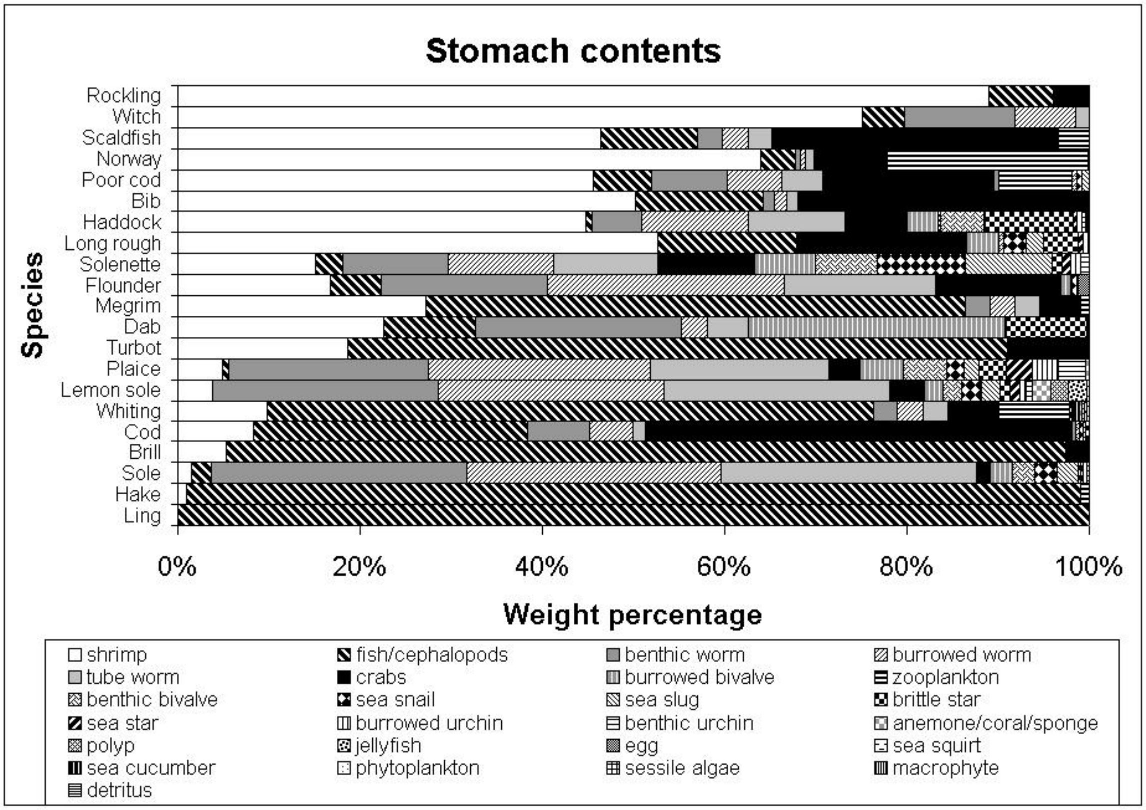
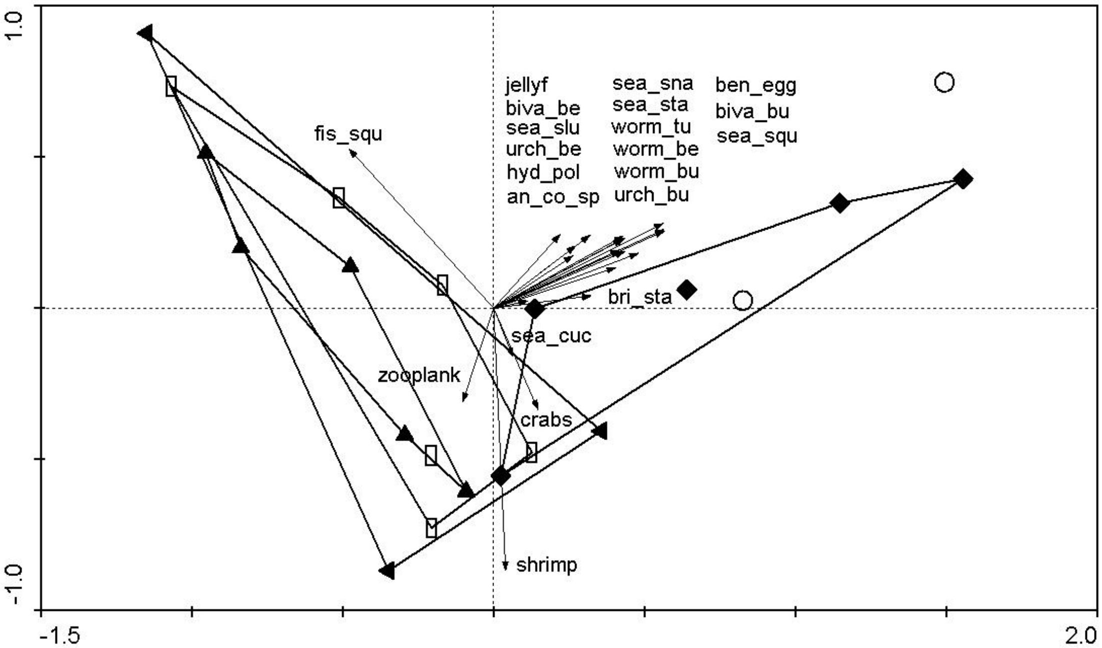


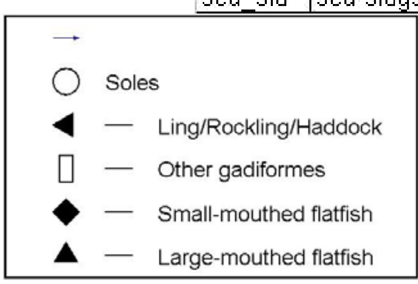
Figure 10. Fish diet. Actual fish diet data obtained from literature. The bars display weight percentages (weight of food type as a percentage of total weight of food in the stomach) of food categories per fish species, representing relative importance.

The three most dominant food categories are (most weight represented in total over all species): shrimp, fish/cephalopods and benthic worms. Species in which the diet consists at least for 50% of fish and cephalopods are: brill, hake, ling, megrim, turbot and whiting. Species in which the shrimp is a diet component that makes up at least 50% of total diet are: bib, rockling, long rough dab, norway pout and witch.



Label	Food category	Label	Food category	Label	Food category
zooplank	zooplankton	worm_bu	burrowed worms	sea_cuc	sea cucumber
ben_egg	benthic eggs	worm_be	benthic worms	biva_bu	burrowed bivalve
hyd_pol	hydropolyps	worm_tu	tube worms	biva_be	benthic bivalve
sea_squ	sea squirts	sea_sta	sea stars	shrimp	shrimp
jellyf	jellyfish	urch_bu	burrowed urchins	crabs	crabs
sea_sna	sea snails	urch_be	benthic urchins	fis_squ	fish/cephalopods
sea_slu	sea slugs	bri_sta	brittle stars	an_co_sp	anemone/coral/sponge

Figure 11. Fish diet PCA. Total variance visualized: 46,9% axis 1; 14,3% axis 2. Stomach content data obtained from literature. Groups defined as morphologically differing are outlined and separated by symbol type.



The diet data were used as an input for a PCA (Fig. 11). After the analysis five groups were projected that were previously defined as morphologically different: *Soles, small-mouthed flatfish, large-mouthed flatfish, ling/rockling/haddock and other Gadiformes*.

The graph shows that *small-mouthed flatfish* hardly overlap with the other groups. They have a diet deviating from that of other species consisting mostly of worms, bivalves and some other sessile animals. *Soles* show a similar diet to *small-mouthed flatfish* also consisting mainly of worms. *Large-mouthed flatfish*, *ling/rockling/haddock* and *other Gadiformes* occupy largely the same area. This group can be seen as two separate groups, one in the upper half of the graph representing fish eaters: ling, hake, brill, whiting, turbot and megrim, and one in the lower half of the graph composed of crab and shrimp eaters: long rough dab, poor cod, bib, norway pout, rockling and scaldfish. Cod has a more or less intermediate position.

3.6 Correlation of predictions with actual diets

<u>Diet spectra correlation:</u>

The results of the correlation of the morphological predictions for each species (the correlation between measurements and specialists) with the actual fish diets per species are given in table 9. The outlined cells indicate the value that correlates the prediction of a species with actual stomach content data of the same species. Those values should be highest according to the expectation as the fish diet from stomach content should match the morphological predictions.

The predictions for bib, brill, cod, rockling, hake, ling, norway pout, turbot and whiting show positive correlations with most or all stomach contents. The predictions for dab, flounder, haddock, lemon sole, plaice, scaldfish, sole and witch show negative correlations with most or all stomach contents.

Striking is that the stomach content of lemon sole shows a maximum positive correlation with the predictions for dab, flounder, haddock, lemon sole, plaice, sole and witch, while it shows a maximum negative correlation with the predictions for brill, cod, rockling, hake, long rough dab, megrim, norway pout, poor cod, turbot and whiting.

The stomach contents of bib, brill, cod, dab, flounder, haddock, long rough dab, megrim, poor cod, scaldfish, solenette and turbot all have the highest correlation with the prediction for cod. Also the stomach contents of bib, dab, rockling, haddock, long rough dab, solenette, turbot and witch show their lowest correlation with the prediction for dab. Most correlations between the predictions of cod, dab and lemon sole and the stomach contents of all species are significant.

Table 9. Diet spectra correlation table. Predicted diet per species (morphology) correlated with actual diet per species (stomach content). Predictions are given in columns and stomach contents in rows. Italics indicate highest and lowest values per row; highest and lowest values per column are underlined; significant values ($p<0.05$; $r>0.44$) are in bold script.

fish species	Bib	Brill	Cod	Dab	Rockling	Flounder	Haddock	Hake	Ling	Long rough dab	Lemon sole
St_Bib	0.406	0.248	***0.738***	***-0.776***	**0.566**	-0.356	-0.325	**0.643**	0.375	0.239	**-0.765**
St_Brill	0.302	0.207	***0.615***	**-0.633**	**0.521**	-0.413	-0.375	**0.574**	0.151	0.316	***-0.637***
St_Cod	**0.447**	0.263	***0.728***	**-0.650**	**0.536**	-0.197	-0.369	**0.599**	**0.442**	0.068	***-0.670***
St_Dab	0.364	0.240	***0.560***	***-0.578***	0.393	-0.408	-0.155	0.310	0.314	0.101	**-0.560**
St_Rockling	0.279	0.163	**0.532**	***-0.716***	**0.474**	**-0.445**	-0.205	**0.517**	0.199	0.345	**-0.675**
St_Flounder	0.392	0.370	***0.693***	**-0.571**	0.374	-0.290	-0.346	**0.443**	**0.499**	-0.021	***-0.604***
St_Haddock	0.239	0.211	***0.529***	***-0.593***	0.407	-0.210	-0.204	0.358	**0.474**	0.029	**-0.540**
St_Hake	0.249	0.198	**0.538**	**-0.562**	**0.480**	-0.415	-0.373	**0.526**	0.080	0.339	***-0.572***
St_Ling	0.250	0.181	**0.524**	**-0.529**	**0.451**	-0.375	-0.347	**0.493**	0.097	0.288	***-0.537***
St_Long rough dab	0.438	0.215	***0.747***	***-0.826***	**0.652**	-0.341	-0.228	**0.590**	0.409	0.214	**-0.787**
St_Lemon sole	0.206	0.119	0.244	-0.058	-0.073	0.080	-0.061	-0.016	*0.384*	*-0.394*	-0.077
St_Megrim	0.360	0.289	***0.738***	**-0.790**	**0.608**	**-0.531**	**-0.448**	**0.687**	0.227	0.386	***-0.793***
St_Norway pout	0.184	0.253	**0.462**	**-0.643**	**0.496**	**-0.502**	-0.357	**0.573**	0.051	**0.528**	***-0.652***
St_Poor cod	0.352	0.315	***0.663***	**-0.721**	**0.549**	**-0.433**	-0.380	**0.606**	0.279	0.333	***-0.739***
St_Plaice	0.248	0.249	0.395	-0.244	0.115	-0.001	-0.165	0.125	***0.584***	*-0.372*	-0.247
St_Scaldfish	0.362	0.283	***0.701***	**-0.746**	**0.553**	-0.390	-0.371	**0.657**	0.325	0.304	***-0.750***
St_Sole	0.242	0.285	0.392	-0.193	0.099	-0.079	-0.204	0.091	***0.444***	*-0.272*	-0.229
St_Solenette	**0.482**	0.276	***0.680***	***-0.564***	**0.455**	-0.084	-0.165	0.291	**0.624**	-0.224	**-0.559**
St_Turbot	0.355	0.230	***0.702***	***-0.737***	**0.587**	**-0.444**	-0.394	**0.652**	0.214	0.339	**-0.734**
St_Whiting	0.317	0.272	**0.668**	**-0.689**	**0.579**	**-0.487**	-0.472	**0.661**	0.140	0.401	***-0.713***
St_Witch	0.274	0.207	**0.509**	***-0.671***	0.403	**-0.493**	-0.218	**0.456**	0.207	0.303	**-0.643**

fish species	Megrim	Norway pout	Poor cod	Plaice	Scaldfish	Sole	Solenette	Turbot	Whiting	Witch
St_Bib	0.380	0.376	0.242	-0.438	-0.268	-0.316	0.071	**0.631**	**0.594**	-0.419
St_Brill	0.339	0.271	0.200	**-0.474**	-0.196	-0.218	0.182	**0.599**	**0.459**	-0.347
St_Cod	0.205	0.264	0.000	-0.318	-0.312	-0.334	0.028	**0.712**	**0.450**	-0.283
St_Dab	0.254	0.286	0.223	**-0.485**	-0.168	-0.040	0.262	0.361	0.389	-0.290
St_Rockling	**0.442**	0.380	0.419	**-0.471**	-0.176	-0.187	0.161	0.397	***0.576***	**-0.450**
St_Flounder	0.224	0.250	-0.038	-0.424	-0.200	-0.127	0.104	**0.585**	0.393	-0.272
St_Haddock	0.226	0.268	0.157	-0.286	-0.226	-0.102	0.129	0.313	0.409	-0.356
St_Hake	0.343	0.255	0.201	**-0.468**	-0.135	-0.205	0.162	***0.547***	0.419	-0.313
St_Ling	0.289	0.218	0.159	-0.429	-0.157	-0.173	0.180	***0.527***	0.377	-0.289
St_Long rough dab	0.330	0.429	0.348	-0.410	-0.287	-0.314	0.121	**0.534**	**0.609**	**-0.489**
St_Lemon sole	-0.160	-0.098	-0.326	-0.025	-0.227	0.203	0.163	0.133	-0.037	0.071
St_Megrim	**0.475**	0.377	0.281	**-0.610**	-0.198	-0.266	0.178	**0.693**	**0.604**	**-0.442**
St_Norway pout	**0.625**	**0.468**	**0.453**	**-0.534**	0.048	-0.391	-0.096	**0.455**	***0.626***	-0.404
St_Poor cod	**0.513**	**0.460**	0.311	**-0.519**	-0.092	-0.389	-0.052	**0.584**	**0.628**	-0.387
St_Plaice	-0.093	0.063	-0.240	-0.111	-0.221	0.103	0.099	0.245	0.112	-0.094
St_Scaldfish	**0.451**	0.401	0.256	**-0.470**	-0.183	-0.365	-0.010	**0.642**	**0.613**	-0.412
St_Sole	-0.024	0.055	-0.234	-0.205	-0.119	0.073	0.104	0.277	0.086	-0.048
St_Solenette	0.048	0.325	0.036	-0.218	-0.275	-0.192	0.059	0.376	0.365	-0.242
St_Turbot	0.387	0.326	0.244	**-0.512**	-0.235	-0.264	0.176	**0.661**	**0.543**	-0.407
St_Whiting	**0.460**	0.344	0.234	**-0.565**	-0.141	-0.306	0.106	***0.683***	**0.551**	-0.375
St_Witch	**0.449**	0.358	0.378	**-0.532**	-0.136	-0.097	0.208	0.369	***0.545***	-0.423

Food partitioning correlation:

Ook hier is uitleg nodig hoe je de correlaties kunt interpreteren.
The correlations between morphological predictions on food partitioning for each food specialist with the actual food partitioning of each food category as found in stomach contents are shown in table 10.

Since the food categories phytoplankton, sessile algae, macrophytes and detritus were not found to be part of the stomach contents for any of the considered species, there were no correlation values for those food categories and therefore they were omitted from the table. The predicted food partitioning for each food specialist in the above categories was still included tough.
The predicted partitioning of detritus, sea squirts, jellyfish, sea cucumber and anemone/coral/sponge show positive correlations with the actual partitioning for all food categories except for zooplankton, shrimp, crabs and fish/cephalopods. The opposite is true for the predictions for shrimp ambush- and pursuit hunters as well as pursuit hunters. They show negative correlations with all food types except for zooplankton, shrimp, crabs and fish/cephalopods.

Summary

Table 11a summarizes the correlations between the predicted diet of species and the actual diet of that species and table 11b shows the correlations between predicted food partitioning of specialists with the actual food partitioning of the corresponding food category. Relative fits are also given for each correlation, indicating the relative weight of the correlation.

Cod, rockling, hake, megrim, norway pout, turbot and whiting are all significantly positively correlated with their respective stomach content data. Cod and norway pout show best predictions for their diet compared to the diet of other species. Dab is the only species that shows a significant negative correlation.
As for food partitioning, the zooplankton townet, burrowed bivalve, ambush hunter and anemone/coral/sponge specialists show significant positive correlations to their respective actual partitioning. Zooplankton townet and ambush hunter specialists show maximum correlations with their corresponding food categories compared to all other food categories. Best relative fits are shown by zoo-townet, zoo-pump, burrowed worm, tube worm, pursuit hunter, ambush hunter and burrowed fish.

Table 10. Food partitioning correlation table. Predicted food partitioning per specialist (morphology) correlated with actual food partitioning per food category (stomach contents). Predictions are given in columns and stomach contents in rows. Italics indicate highest and lowest values per row; highest and lowest values per column are underlined; significant values ($p<0.05$; $r>0.44$) are in bold script.

food category	phyto-townet	phyto-pump	sessile-algae	macro-phyte	detritus	zoo-townet	zoo-pump	egg	polyp	sea-squirt	jellyfish	sea-snail	sea slug	burrowed-worm	benthic-worm	tube-worm
St_zooplankton	0.434	-0.043	0.061	-0.424	-0.293	**0.535**	0.253	0.404	-0.287	**-0.498**	**-0.593**	-0.278	***0.537***	**-0.566**	-0.028	**-0.590**
St_egg	-0.211	-0.001	0.009	0.218	0.054	-0.253	-0.131	-0.194	0.154	0.241	0.273	***0.528***	-0.169	0.053	-0.136	0.137
St_polyp	0.051	0.343	***0.563***	0.349	0.355	-0.054	0.146	0.075	0.400	0.426	0.419	0.123	-0.155	0.118	-0.050	0.167
St_sea squirt	0.069	0.218	*0.437*	0.238	0.165	-0.011	0.085	-0.016	0.287	0.292	0.278	0.085	-0.110	0.025	-0.081	0.071
St_jellyfish	0.066	0.276	***0.477***	0.274	0.287	-0.026	0.114	0.061	0.317	0.331	0.312	0.109	-0.090	0.071	-0.059	0.115
St_sea snail	-0.319	-0.123	0.032	**0.564**	0.412	**-0.449**	-0.400	***-0.489***	0.397	***0.597***	**0.556**	0.310	**-0.460**	0.360	-0.420	0.096
St_sea slug	-0.290	-0.130	0.017	**0.525**	0.401	-0.414	-0.386	**-0.462**	0.367	***0.561***	**0.523**	0.253	**-0.442**	0.358	-0.396	0.087
St_burrowed worm	-0.406	-0.034	0.437	**0.750**	**0.590**	**-0.544**	-0.364	-0.339	**0.674**	***0.804***	**0.759**	**0.578**	**-0.443**	0.435	-0.277	0.249
St_benthic worm	-0.384	0.021	**0.513**	**0.782**	**0.649**	**-0.517**	-0.303	-0.254	**0.740**	***0.851***	**0.815**	**0.521**	**-0.443**	**0.471**	-0.210	0.280
St_tube worm	-0.369	-0.010	**0.464**	**0.726**	**0.623**	**-0.513**	-0.342	-0.308	**0.653**	***0.792***	**0.739**	**0.515**	**-0.444**	**0.452**	-0.278	0.244
St_sea star	-0.212	0.076	0.286	**0.576**	0.428	-0.370	-0.241	-0.384	**0.475**	***0.608***	**0.602**	0.433	**-0.458**	0.198	**-0.463**	0.070
St_burrowed urchin	-0.245	0.022	0.239	**0.568**	0.404	-0.394	-0.284	-0.410	**0.458**	***0.593***	**0.584**	**0.450**	**-0.451**	0.203	***-0.464***	0.065
St_benthic urchin	-0.278	-0.009	0.247	**0.579**	0.409	-0.423	-0.313	-0.410	**0.470**	***0.603***	**0.589**	**0.471**	-0.433	0.229	-0.433	0.093
St_brittle star	-0.158	0.252	**0.551**	***0.615***	**0.444**	-0.278	-0.019	-0.119	**0.579**	**0.611**	**0.549**	0.313	-0.236	0.083	-0.302	0.027
St_sea cucumber	-0.205	-0.090	*0.317*	0.274	0.045	-0.191	-0.119	-0.037	0.252	0.159	0.006	0.135	0.234	-0.085	-0.025	-0.097
St_burrowed bivalve	-0.270	0.164	**0.467**	**0.703**	**0.574**	-0.398	-0.141	-0.185	**0.640**	***0.759***	**0.729**	0.387	-0.396	0.310	-0.279	0.167
St_benthic bivalve	-0.415	-0.140	0.237	***0.692***	**0.471**	***-0.544***	**-0.443**	**-0.462**	**0.540**	**0.691**	**0.609**	**0.445**	-0.379	0.344	-0.396	0.111
St_shrimp	0.214	0.117	0.065	0.056	-0.117	0.326	0.335	0.352	0.077	-0.032	-0.169	-0.058	***0.447***	**-0.485**	-0.097	**-0.576**
St_crab	-0.063	-0.038	-0.093	0.030	-0.092	-0.011	0.026	0.082	-0.092	-0.058	-0.169	0.105	*0.373*	-0.221	-0.058	-0.195
St_fish/cephalopods	0.107	-0.157	**-0.479**	***-0.675***	-0.375	0.134	-0.057	-0.063	**-0.641**	**-0.621**	**-0.460**	-0.385	-0.073	0.127	0.318	0.305
St_anemone/coral/sponge	-0.006	0.320	**0.551**	0.408	0.363	-0.127	0.083	-0.009	0.436	**0.476**	**0.481**	0.270	-0.209	0.104	-0.135	0.171

food category	sea star	burrowed-urchin	benthic-urchin	brittle-star	sea-cucumbe	burrowed-bivalve	benthic-bivalve	shrimp-pursuit	shrimp-ambush	crab	burrowed-crab	pursuit-hunter	ambush-hunter	burrowed-fish	anemone/coral/sponge
St_zooplankton	-0.017	-0.090	-0.382	-0.223	***-0.637***	-0.363	-0.318	**0.456**	0.331	-0.095	**-0.442**	0.421	0.176	-0.403	**-0.534**
St_egg	0.133	-0.075	0.196	0.412	0.287	0.057	**0.447**	-0.280	-0.267	0.313	0.335	*-0.372*	-0.264	0.081	0.255
St_polyp	-0.213	0.261	**0.511**	0.121	**0.448**	0.368	0.389	-0.520	***-0.546***	-0.187	-0.159	**-0.514**	**-0.502**	-0.336	0.431
St_sea squirt	-0.112	0.221	0.421	0.106	0.317	0.186	0.295	-0.335	*-0.374*	-0.105	-0.128	-0.341	-0.352	-0.330	0.308
St_jellyfish	-0.200	0.239	0.427	0.122	0.349	0.299	0.327	-0.411	***-0.449***	-0.150	-0.147	-0.411	-0.422	-0.311	0.332
St_sea snail	-0.040	-0.011	0.109	0.251	0.379	0.272	0.261	-0.117	-0.296	**-0.440**	-0.141	-0.162	-0.281	-0.162	**0.547**
St_sea slug	-0.055	0.006	0.097	0.206	0.348	0.259	0.220	-0.085	-0.267	***-0.472***	-0.165	-0.127	-0.251	-0.158	**0.510**
St_burrowed worm	-0.024	0.290	**0.463**	**0.452**	**0.593**	**0.563**	**0.668**	**-0.518**	**-0.669**	-0.259	-0.025	**-0.582**	***-0.681***	-0.351	**0.785**
St_benthic worm	-0.129	0.337	**0.501**	0.387	**0.618**	**0.637**	**0.695**	**-0.596**	***-0.744***	-0.330	-0.078	**-0.647**	**-0.744**	-0.356	**0.834**
St_tube worm	0.005	0.316	**0.468**	0.407	**0.581**	**0.559**	**0.603**	**-0.495**	**-0.651**	-0.346	-0.091	**-0.558**	***-0.661***	-0.402	**0.767**
St_sea star	0.067	0.097	0.374	0.335	**0.482**	0.312	**0.473**	-0.357	***-0.472***	-0.225	-0.051	-0.407	**-0.467**	-0.290	**0.595**
St_burrowed urchin	0.106	0.089	0.346	0.349	**0.460**	0.290	**0.459**	-0.319	-0.439	-0.200	-0.024	-0.371	-0.438	-0.266	**0.579**
St_benthic urchin	0.116	0.124	0.369	0.376	**0.478**	0.314	**0.475**	-0.329	***-0.454***	-0.180	-0.003	-0.382	**-0.453**	-0.263	**0.592**
St_brittle star	-0.056	0.025	0.285	0.246	0.414	0.399	0.379	**-0.462**	***-0.533***	-0.213	-0.239	**-0.483**	**-0.526**	-0.409	**0.605**
St_sea cucumber	0.056	-0.017	-0.081	0.200	0.004	0.194	-0.014	-0.013	-0.072	0.081	-0.193	-0.035	-0.129	*-0.340*	0.154
St_burrowed bivalve	-0.084	0.097	0.368	0.276	**0.545**	**0.483**	**0.493**	**-0.522**	***-0.635***	-0.360	-0.185	**-0.548**	**-0.604**	-0.318	**0.736**
St_benthic bivalve	0.043	0.092	0.226	0.388	**0.456**	0.406	0.377	-0.237	-0.424	-0.326	-0.134	-0.293	-0.430	-0.311	**0.652**
St_shrimp	**-0.584**	**-0.506**	***-0.593***	-0.128	**-0.508**	0.011	-0.031	0.115	0.000	-0.134	**-0.458**	0.124	-0.093	-0.143	-0.151
St_crab	0.008	***-0.510***	-0.419	0.129	-0.147	-0.134	-0.207	0.197	0.120	0.033	-0.198	0.205	0.107	-0.057	-0.125
St_fish/cephalopods	**0.543**	0.220	0.130	-0.240	-0.044	**-0.458**	**-0.479**	0.363	**0.564**	0.294	**0.448**	0.392	***0.638***	0.413	**-0.521**
St_anemone/coral/sponge	-0.124	0.257	***0.577***	0.236	**0.513**	0.365	**0.500**	**-0.570**	***-0.599***	-0.085	-0.059	**-0.575**	**-0.558**	-0.321	**0.490**

Table 11. Summarized correlations and relative fits for diet spectra and food partitioning. Correlations are taken from the earlier correlation tables and relative fits are calculated as the percentage of the total correlation range for a particular prediction – stomach content combination. Significant positive correlations are printed in bold script.

Table 11a. Diet spectra correlations for each fish species with the corresponding stomach content.

DIET SPECTRA		
Fish species	Correlation	Relative fit
Bib	0.406	74
Brill	0.207	35
Cod	**0.778**	**100**
Dab	-0.578	32
Rockling	**0.474**	**75**
Flounder	-0.290	39
Haddock	-0.204	65
Hake	**0.526**	**77**
Ling	0.097	8
Long rough dab	0.214	66
Lemon sole	-0.077	100
Megrim	**0.475**	**81**
Norway pout	**0.468**	**100**
Poor cod	0.311	82
Plaice	-0.111	85
Scaldfish	-0.183	36
Sole	0.073	78
Solenette	0.059	43
Turbot	**0.661**	**91**
Whiting	**0.551**	**88**
Witch	-0.423	12

Table 11b. Food partitioning correlations for each food specialist with the corresponding food category.

FOOD PARTITIONING		
Food-specialist	Correlation	Relative fit
zoo-townet	**0.535**	**100**
zoo-pump	0.253	89
egg	-0.194	33
polyp	0.400	75
sea squirt	0.292	62
jellyfish	0.312	64
sea snail	0.310	72
sea slug	-0.442	2
burrowed worm	0.435	97
benthic worm	-0.210	32
tube worm	0.244	93
sea star	0.067	58
burrowed urchin	0.089	71
benthic urchin	0.369	82
brittle star	0.246	70
sea cucumber	0.004	51
burrowed bivalve	**0.483**	**86**
benthic bivalve	0.377	73
shrimp pursuit	0.115	68
shrimp ambush	0.000	57
crab	0.033	64
burrowed crab	-0.198	29
pursuit hunter	0.392	97
ambush hunter	**0.638**	**100**
burrowed fish	0.413	100
anemone/coral/sponge	**0.490**	**75**

Another way of comparing diet predictions with the actual diets was to construct tree diagrams. A rootless tree structure approach was chosen to identify the largest groups. Figure 12 shows the results of the analysis of the morphological predictions. The cluster tree of the predictions is similar to the PCA diagram of the predictions in most areas, clustering *small-mouthed flatfish* in one group and *soles* in another, apart from *large-mouthed flatfish* and any Gadiformes. However differences must be noted: in the cluster analysis bib and haddock appear much alike, this is less so in the PCA graph or in the correlation graph. Also in the cluster tree, *large-mouthed flatfish* and most Gadiformes occur mixed; again this is not seen in the PCA graph. The clusters *ling/rockling/haddock* and *other Gadiformes* are no longer present in the cluster diagram; however ling and haddock still appear to be deviating from other groups.

The cluster analysis of the stomach content data (Figure 13) shows the following groups:

1. **Piscivores:** cod, brill, ling, hake, whiting, turbot and megrim. This group contains all species that have a diet dominated by fish. With a possible exception for cod that also eats many crustaceans. All members of this group either belong to the *large-mouthed flatfish* or to the Gadiformes.
2. **Crustacean-eaters:** bib, scaldfish, poor cod, norway pout, long rough dab, rockling, witch and haddock. In this group shrimp and crabs dominate the diet. Members of this group belong to the Gadiformes, the *large-mouthed flatfish* and one to the *small-mouthed flatfish*.
3. **Worm-, bivalve- and echinoderm-eaters:** dab, solenette, flounder, plaice, sole and lemon sole. This group contains both *soles* and almost all *small-mouthed flatfish*.

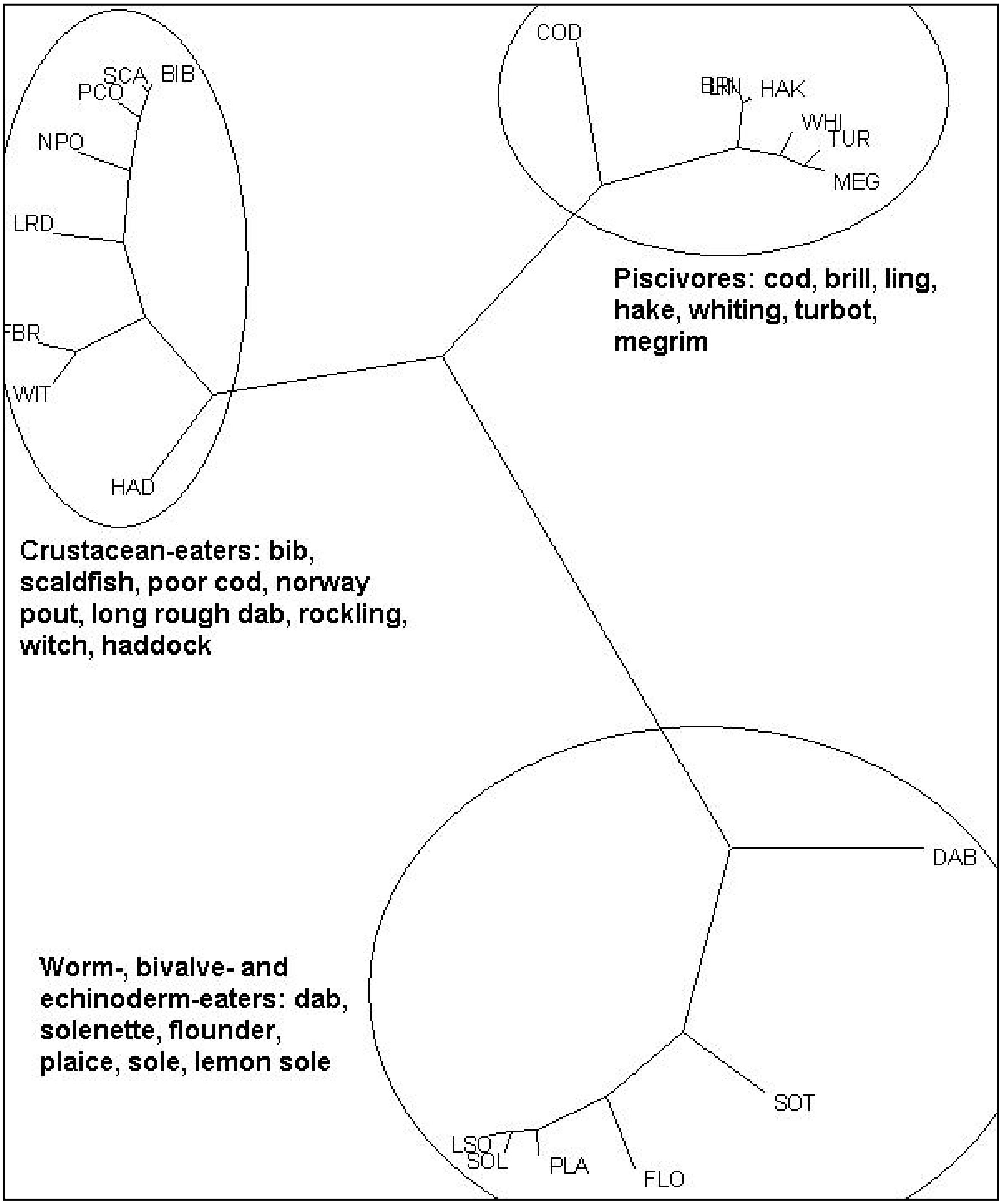


Figure 12. Cluster analysis of morphological predictions. Shown is an unrooted tree resulting from an UPGMA clustering of a product-moment correlation. Large clusters are encircled.

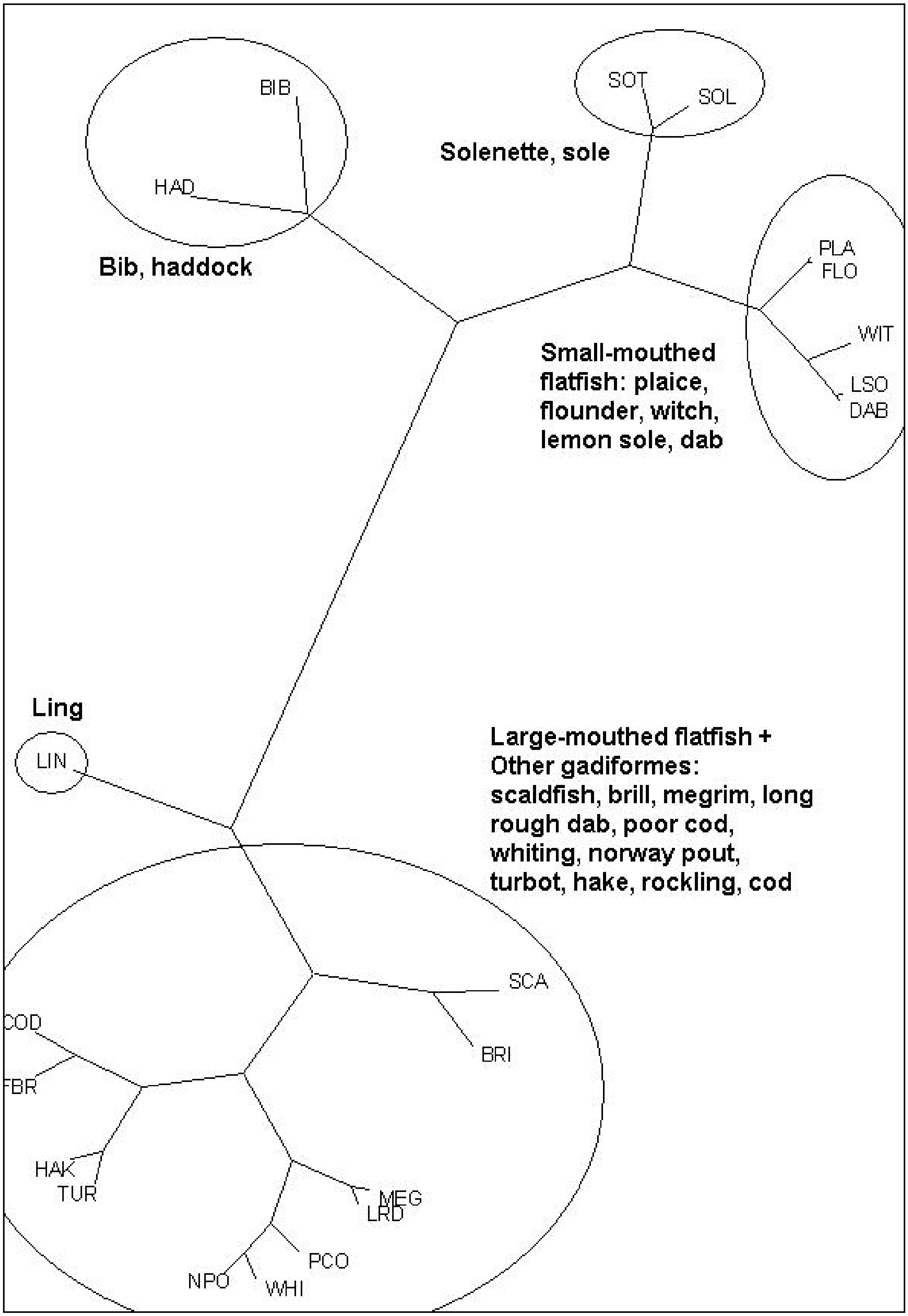


Figure 13. Cluster analysis of stomach contents. Shown is an unrooted tree resulting from an UPGMA clustering of a product-moment correlation. Large clusters are encircled.

4 DISCUSSION & CONCLUSIONS

The goal was to answer the question whether fish diet can be predicted from morphological parameters. Concluding the answer is that the diet of some fish can be predicted fairly well: the stomach content of the *large-mouthed flatfish* and *other Gadiformes* groups show many significant correlations with the predictions that were done for them and those correlations mostly fit best for species themselves. The same holds for the large and/or fast food types, the partitioning of which is predicted to a higher degree than other food types.

However, for the *soles* and for *small-mouthed flatfish* the method did not succeed in predicting the diet. The predictions showed low or even negative correlations with the stomach contents of the species in these groups, and the stomach contents correlated higher with species in the other groups (*other Gadiformes* for example).

This means that for 'hunters', or fish that feed primarily on fish and/or large crustaceans the predictions were better than for polychaete and bivalve eaters.

Five clusters of morphotypes were identified (Figures 8b, 13): *soles* (long barbels, no gill rakers, small eyes and mouth, limited suction capacity, long gut), *small-mouthed flatfish* (small mouth, biting/scraping teeth), *large-mouthed flatfish* (large mouth, long rakers, high suction capacity, short gut), *ling/rockling/haddock* (long barbels, few/small rakers) *and other Gadiformes* (high suction capacity, large mouth, short gut). When looking at diet data these morphotypes cluster differently (Figures 12, 13): *Soles* and *small-mouthed flatfish* appear similar, but different from the groups: *large-mouthed flatfish, ling/rockling/haddock and other Gadiformes*, which show great similarity with each other. The morphological predictions appear unable to discern between fish eaters and large crustacean eaters within the *Large-mouthed flatfish* and both Gadiformes groups, i.e. they are all seen as 'hunters of large/fast prey' in the clusters found (both in the tree as well as in the PCA). Roughly, *Large-mouthed flatfish* and both groups of Gadiformes can be divided into two groups: piscivores, containing the largest species, and crustacean-eaters, containing the smaller species.

The causes for the discrepancy between predictions of diet and stomach content data can be both biological and methodological. In order to trace these causes, the steps taken in this method, and their consequences, are reviewed consequently:

Diet data: The step in which stomach content was compared to morphological predictions was taken using stomach content data from literature. This limits the power of this ´control step´ in several ways. First the literature does not always determine stomach content to the maximum (species) level. This is problematic in that often this led to over- or underestimates of food categories predetermined in this method. Worms for example were divided into three (functional) categories for this study: burrowed-, tube- and benthic worms, but literature in some cases only identified to the level of Polychaetes and Nemerteans for instance. This may have led to overestimation of worms in the stomach control data, possibly partially explaining the poor prediction in their food partitioning. Second, as the North Sea is heavily fished, competition may be reduced (Rice and

Kronlund 1997) and species may share similar food resources even if they are not well specialised (Liem 1980). In this situation, the observed diet could deviate from the predicted diets. Third, when predicting diet from a bottom-up perspective, starting at food and its functional properties, relative abundances were left out of consideration. Therefore when species are well equipped morphologically to specialize in one or more particular food categories, they might still not do so because the food category is not encountered often enough. *Small-mouthed flatfish* and *soles* were the only groups equipped with teeth types other than pointed. This means that food categories demanding those teeth types are predicted to be the main prey for those groups and that, of all fishes, they are best capable of handling this prey type. However, if those food categories are not plentiful in the habitat of the species, then the fish must switch to its ‘morphologically sub-optimal’ feeding, which is in that case ecologically optimal. Some resources may be so abundant and/or easy to obtain (maybe only at certain times) that all predators in the system, in this case all fish, take them when given a chance, even if their morphology is not optimally suited to tackle this food category (Robinson and Wilson 1998).
One exception deserves special notice: the stomach content data for ling was based on only seven individuals. This information was solidified by personal communication with N. Daan and by referring to the book: ‘A key to the Fishes of Northern Europe’ (Wheeler 1978), nonetheless the stomach contents were not based on hard data, making the control of the prediction for ling unreliable.

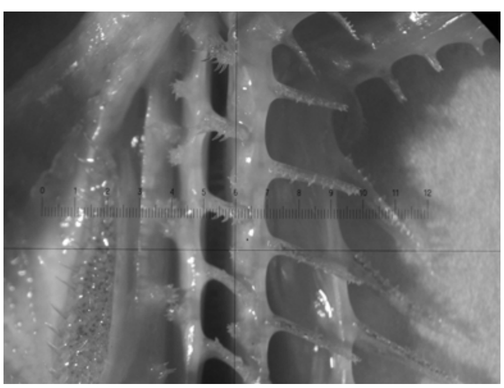
Generating predictions: Could the incongruity between some predicted and actual diets be explained by flawed predictions? The predictions start with the definition of specialists and this was done on a comparable basis as well. This step made a distinction between many food types and this makes detailed predictions on diet possible. Again this may have led to over- or underestimation of food categories in the stomach data, when food categories are abundant or scarce. Also assumptions were made when creating specialists from food categories on feeding behaviour. Food categories were transformed into one or more ‘feeding behaviours’. Fish and cephalopods for example were subdivided into burrowed fish-, ambush hunting- and pursuit hunting specialists. These assumptions were based on the work by Sibbing and Nagelkerke (2001), but may not fully apply to the North Sea fish studied.

The choice of specialists was made to represent the total width of food categories present in the entire North Sea, to cover all diet options. Some food categories, such as phytoplankton or macrophytes were not eaten by any of the studied species (these items were not found in the stomach contents). However this may have any number of reasons, maybe phytoplankton and macrophytes (or macro algae) are not common in the North Sea, a reason for them not to be eaten. Nevertheless, what this method does is predict which fish species would be best suited to handle those type of resources should they be available.

One important aspect, prey size, was only roughly taken into account when determining demands for specialists (plankton was considered so small that it needed filtering systems to be eaten for example). This is because many food categories could vary extremely in size, ranging from below one millimetre to a metre. Consequently all fish used for the study could, in theory, eat all food categories. However, the assumptions that some food items always require biting and others always require suction feeding proved incorrect in some cases. Sea stars and sea cucumbers for example were transformed into biting specialists, whereas those items, when found in the stomachs, were often so small, in some cases only half a millimetre in diameter (Mattson 1992), that they could be swallowed whole by either particular suction, filter feeding or accidental feeding. Hence, the demands for biting were incorrectly imposed and led to false predictions.

The second part that constitutes the predictions is formed by the morphological measurements. Measurements were done on only few fish, 3-5 specimens per species. Despite the small sample size, it was clear that the intra-specific variance was generally far less than the inter-specific variance. Hence, measurements errors are an unlikely cause for false predictions. The third, and also very important, part of predicting diet is the set of morphological variables measured. Their strengths are first that there were many variables used in the analysis, several of which had a similar function in feeding. Although this suggests that at least some of those variables might be redundant, this is not necessarily the case as each variable carries an amount of noise with its signal, and multiples will more likely result in reducing this noise (Sibbing and Nagelkerke 2001); secondly most variables were used already in the article of Sibbing and Nagelkerke (2001) and had proven their predictive power. And although this was only the case for cyprinid fish, this still holds true for all fish as the variables are based purely on functional morphology. An equally large and strong mussel will not be cracked more easily in the North Sea than in Lake Tana.

Some variables need special discussion. The variables ‘Gill raker length’ and ‘Gill interraker distance’ were used to segregate plankton-eating specialists from large prey-eating specialists, plankton-specialists needing many long rakers in contrast to hunters of large prey that require only a few rakers that are as short as possible to reduce resistance. However, De Groot (1971) states that ‘gill rakers are indispensable to fish feeders, since they prevent the prey, grasped alive, to struggle out of the mouth’, hereby referring to the long teethed rakers possessed by piscivorous flatfish. This might cause false predictions and could make interpretation of the results more difficult.


A photograph showing the toothed gill rakers of megrim (*Lepidorhombus whiffiagonis*).

Body depth was measured in roundfish as body height, but in flatfish as body thickness.

To interpret this difference the function of body depth must be assessed: deeper bodies allow fish to be more manoeuvrable but less fast (Keast and Webb 1966; Webb 1982; Webb 1984), in other words fish with deep bodies have increased performance in eating prey that is difficult to access, while fish with lower bodies are better cruisers. Using this division, according to this study the flattened body of flatfish inhibits their ability in pitching their body and therefore their ability to access food items on the bottom easily. However flatfish bend to their lateral side when reaching to the bottom with their mouths and do not need to rotate their entire body around a horizontal axis and this mechanism is fundamentally different from the pitching that roundfish have to do.

Looking at individual species, the diet is only well predicted for species that hunt for relatively large and fast prey. This group contains all Gadiformes and the *large-mouthed flatfish* and it was found to be morphologically different from the other species. An explanation for these comparatively accurate predictions is that ambush- and pursuit hunting and the powerful suction that is associated with these foraging behaviours make large demands on fish morphology. Many of the morphological variables measured on the fish make clear distinctions between these hunters and other specialists; examples are caudal peduncle depth, caudal fin aspect ratio, teeth types, body depth, orbital length and a variety of variables describing suction performance in fish (for references see materials and methods). The large prey-hunter group can be divided into two subgroups: piscivores and crustacean-eaters. Moreover, on the basis of the predictions large-mouthed flatfish should have shown a smaller portion of shrimp in their stomachs as opposed to Gadiformes. According to the stomach contents however large-mouthed flatfish, in particular scaldfish and long rough dab, show that shrimp form a large part of their food.

The results show that in general the bigger predators in this group: brill, ling, hake, whiting, turbot and megrim associate more with piscivory and the smaller predators: bib, scaldfish, poor cod, norway pout, long rough dab, rockling and witch show a greater part of crustaceans in the stomach, with the exception of cod and haddock, which are large predators that appear to be intermediate in this respect. Apparently larger species are more successful in hunting fish and cephalopods than smaller species. When considering that fish are generally larger prey than crustaceans, this could be explained, because larger hunters have larger gapes and are relatively faster. However, this study did not take the difference in prey size between crustaceans and fish/cephalopods into account because these overlap and because predator sizes can vary greatly as well. However, Sibbing and Nagelkerke (2001) conclude that after prey velocity, prey size is the most important selection criterion for fish to be able to eat the prey. This may well explain that smaller species eat more shrimp than fish. In spite of this, the morphology makes no distinction between these small and large predators. Both have equal relative gape sizes, so even if prey size were taken into account, the predictions would still show little or no distinction between piscivores and crustacean-eaters. A suggestion in this case could be to include maximum length of the predator as a morphological variable. Another option is to assess the trophic level of fish using nitrogen stable-isotope analysis (Jennings et al. 2002) and use this as a variable, although this would void the whole point of assessing a fish community strictly through functional morphology.

There is another possible explanation for stomach contents not matching with morphological predictions in the case of a) the predicted difference in diets between large-mouthed flatfish and Gadiformes; and b) the unpredicted difference between piscivores and crustacean-eaters. It may be that shrimp eating was split into two feeding strategies (ambush- and pursuit hunting) only. Because ambush- and especially pursuit hunting make such large demands on fish morphology, this may have caused fish predicted as relatively poor hunters to be predicted as poor shrimp eaters as well, while in reality maybe shrimp eating is also well covered by the slow swimming, particulate suction feeding strategy. In other words: combining all forms of shrimp into one or two food types might be far too limiting. Norton explains that suction feeding results in high predation success on shrimp (Norton 1991). He also states the same for ram feeding, a feeding mode requiring fast swimming; meaning the ambush- and pursuit hunting techniques are also viable. The difference in diet predicted between Gadiformes and *large-mouthed flatfish* may also be explained by different hunting techniques. Lagardère (Lagardere et al. 2004) states that turbot, an example of the large-mouthed flatfish introduced in this study, feeds exclusively by suction, although this is based on experiments using small artificial fish-feed pellets. Furthermore Gibson (2005) says that flatfish use camouflage to strike at prey. This indicates that large-mouthed flatfish may well lie in wait on the bottom and then suck in their prey at the last possible moment, using little or no forward motion, whereas Gadiformes are free-swimming fish that cannot hide on the bottom as well as flatfish. This might then introduce the particular feeding strategy applying also to shrimp; something not anticipated by the method and possibly one explanation for the difference in morphology between large-mouthed flatfish and Gadiformes in spite of similar diets. Additionally, the *large-mouthed flatfish* were separated morphologically from the Gadiformes by possessing many long gill rakers. According to predictions this makes *large-mouthed flatfish* closer to being plankton-eaters than it does Gadiformes. However the presence of long rakers in large-mouthed flatfish does not necessarily mean that these flatfish can actually forage on plankton by filter feeding. No plankton was found in the stomachs of any of the *large-mouthed flatfish*, this indicates that indeed they do not (filter-) feed on plankton in their mature life. This could be explained if there was no plankton present in their habitat or if these structures really serve a different purpose. The gill rakers found in all large-mouthed flatfish and all Gadiformes were toothed. As said earlier, De Groot (1971) suggests that long toothed gill rakers are indispensable to fish feeders. This suggests that maybe numerous long gill rakers can have functions other than filter feeding.

It was said earlier that body depth was likely measured in an incorrect way in flatfish and that this might have caused poor predictions. Indeed, if the PCA of the morphological measurements is repeated leaving the gill raker- and the body depth variables out, large-mouthed flatfish and other Gadiformes appear much more similar, the only difference then mainly being caused by the barbel length variable (results not shown).

It was also found that witch, a *small-mouthed flatfish*, ate mainly shrimp, and was therefore a member of the crustacean-eating group, while it was predicted to be better equipped to eat harder food items like bivalves and polyp-like animals, similar to other flatfish of this type. However this may largely be attributed to flawed diet data: Rae

(1965), Cargnelli (1999) and Link (2002) found that witch (*Glyptocephalus cynoglossus*) feeds mostly on polychaetes. This would still mean the species would have been predicted rather poorly, however it would put the fish among other small-mouthed flatfish again (also polychaete eaters), likely this would be a more realistic result.

Small-mouthed flatfish and *soles* in general were poorly predicted. Their predicted diet mainly contained food items that are difficult to reduce, both mechanically and chemically. This can be accredited to the morphological specializations that separate them from the other species, namely cutting, crushing and scraping teeth and long guts. In spite of this the diet data showed that most were predominantly polychaete feeders and secondarily bivalve- and crustacean-eaters. Of these the benthic bivalves are hardest to crack and digest (pursuant to the specialist profiles) and accordingly they were predicted best. Worms were predicted to be harder to eat for *small-mouthed flatfish*. Several varied sources were available on the stomach contents of small-mouthed flatfish, so it is highly unlikely that the diet data were unreliable. Perhaps in reality, worms are easily obtained as prey by all fish and are only spurned by fish when they have access to higher quality food? Or maybe the behaviour and unique lifestyle of flatfish causes them to be better adapted at eating worms without this being registered in any of the measured morphological variables? The first question might be partly answered by the effects of bottom trawling. Engel concluded that bottom trawling caused a decrease in benthic fauna diversity – especially sessile animals like bivalves, corals and hydroids (Collie et al. 2000; Jennings, et al. 2001; Rumohr and Krost 1991) but an increase in the abundance of opportunistic species, among which polychaetes that were part of flatfish diet in the area studied (Engel and Kvitek 1998). The North Sea is intensively trawled (Rijnsdorp et al. 1998) and this could explain an abundance of polychaetes. In addition, according to Daan prey size appears to be a key factor in determining whether one prey is valued higher than another (Daan et al. 1990), this could be the reason for the diet shifting to fish and crustaceans as soon as mouth size allows instead of worms in fish that have access to them and that are suited to handle them, for example in Gadiformes. Besides, worm specialists were created as not demanding any extreme values for any of the variables. In contrast, *small-mouthed flatfish* show in some areas morphological extremes when compared to other species that set them apart. They were predicted as specialists on hard, indigestible food items, which demand similar extreme values and this way they may be distanced further from worm specialists than other species. This could possibly result in them to be predicted as poor worm eaters, whilst in reality their extreme morphology does little to impede their capabilities to ingest worms (in concordance with stomach content literature).

The second question was whether the behaviour and unique lifestyle of flatfish causes them to be better adapted at eating worms without this being registered in any of the measured morphological variables. Steven (1930) states that tubicolous polychaetes are successfully hunted by lemon sole because of its unique hunting behaviour. Dab and plaice hunt in a similar fashion to lemon sole, with less success on polychaetes alone, but with a broader diet (Steven 1930), which is supported by the stomach content data. The unique hunting behaviours of these flatfish were not measured by any of the variables, and if worms have few morphological demands, the behavioural aspect becomes of greater importance in explaining foraging performance on them.

A third matter must be addressed as well. No variables were included to account for differences in olfactory sense between species. Although an attempt was made to quantify olfactory sense, this attempt failed for the results were inconsistent with the findings of De Groot (1971) who researched the matter extensively. Because many marine worms are burrowed or living in the sediment (designated burrowed and benthic worms in this study) (Hayward 1999) they may be easier located using smell. The work of De Groot and Steven (De Groot 1971; Steven 1930) provides - circumstantial - evidence of this as they conclude that flatfish relying solely on visual cues (large-mouthed flatfish in this study) are largely piscivores and flatfish utilizing chemical cues feed on polychaetes (the small-mouthed flatfish). A suggestion for further research might be to compare the size of sensory cerebral lobes of all species to see if those show a strong correlation with the use of their respective sensory organs (likely, see also De Groot [1971]).

Overall the predictions seem to be good indicators to separate groups of feeding specialists. Only minor changes are needed to fine-tune morphological measurements. The diet predicted is only correct in hunters of large prey, not for other specialists. Striking is the large variety of feeding morphology in flatfish. Variance in morphological variables among flatfishes was greater than between flatfishes and Gadiformes.

Conclusions:

1. Hunters of large prey (large-mouthed flatfish and all Gadiformes) are generally predicted well;
2. Species predicted to be well adapted to eating food items that are hard to (mechanically and/or chemically) reduce were poorly predicted;
3. Within the group of large-prey hunters morphology fails to distinguish between piscivores and crustacean-eaters;
4. Morphology falsely predicted large-mouthed flatfish and Gadiformes to have different diets;
5. Stomach content data was flawed for some species, which caused the testing of predictions to become unreliable;
6. Knowledge both on the foraging behaviour of flatfish and on their prey is a bottleneck in defining food specialists and predicting diets from morphometrics.

Recommendations for further research

Future research could attempt to simplify the many detailed specialists into large clusters of similar specialists while implementing the few changes suggested. This can result in a more practical prediction tool in predicting potential diets of fish at the cost of detailed knowledge at species level. A large point of uncertainty is the relative abundance of food types in the studied area. This knowledge is absolutely necessary if accurate tests are to be made. If this knowledge is available predictions can be checked more profoundly and the method as it exists now will prove its effectiveness. If proven effective then it is capable of predicting reliable diet spectra for fish species in a diverse system and in this way capable of predicting niche shifts should these occur. Daan and Jennings (Daan, et al. 2005; Jennings et al. 2002) observe a steady increase of smaller fish species and a decline of larger fish species in the North Sea fish community. When large species disappear a smaller member of the fish community could fill their feeding niche. If for example a species with the potential to eat fish efficiently is present in the system but was in the past out-competed by one such larger, more specialized species, it is now potentially capable of taking over the feeding niche of the larger species. Note that this only applies when there is/was competition for the resource.

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