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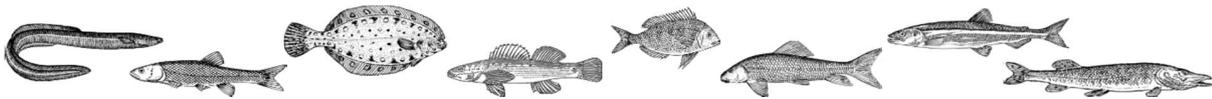
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Shape matters:
Ecomorphology Informs on Functional Traits and Diversity
of Barents Sea Fish



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Structure without function is a corpse and function without structure is a ghost.

Vogel and Wainwright (1969, p. 93)

Executive Summary

The Barents Sea (BS) is an arcto-boreal sea and one of the most productive areas adjacent to the Arctic, hosting many commercial fish stocks. As a result of climate change, temperature increases and a northward movement of several fish species in the BS have been reported, which will likely change community structures and ecosystem functioning. Hence, more information on ecosystem functioning need to be obtained to better understand the fish communities' responses to stress.

Ecomorphology relates shape directly to function. In this study, a landmark-based geomorphometric approach was chosen to assess the shape variation in the 72 most commonly observed fish species of the BS.

The main shape differences were found in the location and the base-length of the anal and dorsal fins as well as in the overall body shape. Through differences in the location and the base length of the anal and dorsal fins, diet and habitat differences were identified as they are adaptations to environmental and ecological factors. Eel-like species as well as flatfish presenting long-based fins are usually associated with a benthic diet and demersal habitats. Small, streamlined fish with short-based anal and dorsal fins are more likely planktivores and pelagics. Biogeographic differences were found in the overall body shape, where eel-like, elongated fish are more often found in the arctic environment. But diet and habitat seemed to be the main drivers for shape variation whereas biogeography and temperature played a less important role.

Functionally, large demersals and flatfish with long-based anal and dorsal fins distribute energy over large temporal and spatial scales and function as important links between lower and higher trophic levels. Eel-like fish with long-based anal and dorsal fins are very efficient in using locally abundant resources. Migratory species with streamlined bodies and short anal and dorsal fins, such as herring and capelin play an important role by transporting energy in the form of resources throughout the system. Such fish are considered key species and are essential for the ecosystem functioning.

In the future, such shape information can find an important application in functional trait matrices to further investigate ecosystem functioning and its resilience and vulnerability. This will be especially important for sustainable management in times of climate change.

Abstract

The Barents Sea (BS) is an arcto-boreal sea and one of most productive areas adjacent to the Arctic, hosting many commercial fish stocks. As a result of climate change, high temperature increases and a northward movement of different species in the BS have been predicted, which will likely change community structures and ecosystem functioning.

Ecomorphology relates shape directly to function. In this study the shape variation in the 72 most commonly observed fish species of the BS was investigated.

Diet and habitat seemed to be the main drivers of shape variation in BS fish whereas biogeography played a less important role. Large demersals and flatfish function as important links between higher and lower trophic levels while eel-like fish are very efficient in using locally abundant resources. Migratory fish, with streamlined bodies are usually key species and essential to ecosystem functioning by transporting energy in the form of resources through time and space. Such shape information are very useful to further investigate ecosystem functioning and its resilience and vulnerability. This will be especially relevant for sustainable management in times of climate change.

Keywords: Functional biodiversity, ecomorphology, landmarks, Barents Sea fish community.

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1. Introduction

The Barents Sea is an open arcto-boreal sea which lies entirely north of the Arctic Circle. It is one of the deepest shelf seas surrounding the Arctic Ocean. The Barents Sea is often considered a pathway and transition zone between the Atlantic and Arctic Ocean, as Atlantic water passes through, entering the Arctic Ocean (Jakobsen & Ozhigin, 2011). It is therefore characterized by three main water masses: (1) Coastal, (2) Atlantic, and (3) Arctic (Jakobsen & Ozhigin, 2011). The same categorization applies for the three Currents of the Barents Sea. The transition area between the warm and saltier Atlantic water and the colder and fresher Arctic water in the Barents Sea is known as the polar front (Jakobsen & Ozhigin, 2011). Parts of the Barents Sea also feature an extensive permanent and seasonal ice cover, though there is a high seasonality in the extent of the ice as it is influenced by both the Atlantic and the Arctic Oceans, as well as by atmospheric conditions (Jakobsen & Ozhigin, 2011).

However, throughout the last decade, it has become more and more clear, that climate change already has, currently is and will be affecting the Barents Sea in the future (e.g. Drinkwater, 2011; Eide & Heen, 2002; Loeng & Drinkwater, 2007; Moritz, Bitz, & Steig, 2002). Drinkwater (2011) synthesizes the different levels and ways in which the Barents Sea is influenced by climate change. He highlights how biological processes in the Barents Sea (a high latitude environment) respond very pronounced to the recent warming and how productivity changes with climate variability. For future climate change scenarios, poleward movements of several species are predicted which will change the community structure and most likely the ecosystem functioning within the Barents Sea (Drinkwater, 2011; Field, Barros, Mach, & Mastrandrea, 2014). Among these northwards moving species, several Barents Sea fish are to be found. Climate variability influences fish indirectly by affecting their biological environment, such as predators, prey and species interactions, as well as habitat type and structure. Also, there are direct impacts on fish physiology, e.g. on metabolic and reproductive processes (Loeng et al., 2005). This, however, gives many reasons for concern, as the Barents Sea is one of the most productive seas adjacent to the Arctic as well as among the most productive fisheries in the world (Eide & Heen, 2002). The Barents Sea serves as an important nursing area and presently contains the largest existing population of Atlantic cod *Gadus morhua* in the North Atlantic (Gjørseter, 2009). The annual yields of fish in the Barents Sea vary between 0.5 and 4.5 million

tons, and fishing pressure is generally high (Nakken, 1998). Besides, many non-commercial fish species exist, as it is known that around 200 different fish from 66 families occur in the Barents Sea, of which around 100 species are commonly observed (Fossheim, Nilssen, & Aschan, 2006; Wiedmann et al., 2014). It is also a system with relatively low biodiversity, but a very high degree of species interaction (Wassmann et al., 2006).

Unfortunately, attention has mostly been focused on commercial species and only during the last few years, more publications have concentrated on the whole fish community in the Barents Sea (Fossheim et al., 2006; Wiedmann et al., 2014). In order to properly assess and manage an ecosystem, information about community structure, functioning and responses to stress need to be evaluated. This is especially important in times of climate change and high fishing activities, which both pose threats by adding pressure to the system (Drinkwater, 2005; Hamre, 1994; Nakken, 1998). Drinkwater (2005) reported how responses of an ecosystem to temperature change include changes in predators and prey. In 2011, Drinkwater predicted structural and functional changes due to changes in species distributions in response to climate change (Drinkwater, 2011). Murawski (1993) also denoted variations in the functional responses of distributions as a result of climate change that will most likely alter trophic relationships among fishes in the ecosystem. Another study suggests an increase in fish productivity and fish are expected to move northwards under climate change scenarios (Stenevik & Sundby, 2007). Loeng and Drinkwater (2007) also report on climate-driven distribution patterns for several fish species, such as cod, herring and blue whiting. The authors inform on northward movements of fish in extended warm periods and southward movements in cool periods. They describe how fish productivity increases through higher abundances and growth rates, as climate change increases primary and secondary production. Concluding climate change influences fish distribution and therefore functioning of an ecosystem. The vulnerability of an ecosystem and how it is going to react to stressors, however, depends on its adaptability, meaning the ability to maintain functions under changing conditions (B. Walker, Kinzig, & Langridge, 1999).

To account explicitly for the functions in an ecosystem performed by fish in the Barents Sea, the measure of functional diversity (FD) has recently been applied (Wiedmann et al., 2014). Functional diversity describes ‘the range and value of those species and organismal traits that influence ecosystem functioning’ (Tilman, 2001). In the study by Wiedmann et al. (2014) functional diversity is used to assess adaptability and vulnerability of the Barents Sea fish

community and the importance of the functioning of fish is highlighted. And in order to determine function, morphology measures can be used. Ecomorphology resembles an approach which relates shape directly to function. Its gist consists of comparing patterns of variation in ecological characteristics with patterns of variation in morphological characteristics in order to establish a functional relationship (Kotrschal & Goldschmid, 1983; Norton, Luczkovich, & Motta, 1995; Smirnov, Makeyeva, & Smirnov, 1995).

In ecomorphological studies on fish, one or more morphological features are simply measured and then related to ecological characteristic, which are either obtained through observations in the field or lab, or through available literature (Chan, 2001; Norton, 1995; Wainwright & Richard, 1995). This will usually be followed by univariate or multivariate analyses and can then be applied as a predictor when relating shape to ecological features and functions or vice versa (Chan, 2001; Norton, 1995; Wainwright & Richard, 1995). However, in modern days where technology is easily accessible and cheap, there is no more need to take measurements on actual fish. A much easier approach is the shape analysis through geometric morphometrics. It is the study of shape variation and its covariation with other variables of interest. The method is landmark-based and retains information on spatial covariation among landmarks (Rohlf & Marcus, 1993). These landmarks can easily be set via computer programs by simply using images or drawings of the species of concern. Today, the internet offers a great variety of sources where one can access images of all sorts of species and most landmark-setting programs can be downloaded for free. This makes the geometric morphometric approach especially fast, easy and cheap, while nevertheless delivering meaningful results. The data in geometric morphometrics is recorded as two- or three-dimensional morphological landmark points. These usually homologous landmarks across species, are then analyzed in the form of coordinates and give the opportunity to evaluate how or where certain structures have moved relative to others (Rohlf & Marcus, 1993). Multivariate statistical analysis then allows for statistical characterization of the morphological variation itself and to test for significant correlations between body shape and ecological traits (Rohlf & Marcus, 1993). Several morphometric studies have already been conducted on fish (A. Loy, Boglione, Gagliardi, Ferrucci, & Cataudella, 2000; Angelo Loy, Mariani, Bertelletti, & Tunesi, 1998; Park, Aguirre, Spikes, & Miyazaki, 2013; Rüber & Adams, 2001; Sarà, Favaloro, & Mazzola, 1999). However, no publications are available so far which considered a fish community as a whole in their analysis.

In this study, a landmark-based geometric morphometric approach was chosen to assess body shapes of the Barents Sea fish community. The main goals were to (1) assess shapes and shape differences of the Barents Sea fish and (2) to combine landmark data with available ecological data in order to analyze correlations between shape and diet, habitat use and biogeographical affiliation. (3) Links between shape and shape patterns to function were drawn and discussed. The importance of shape as a tool to assess ecosystem functioning is highlighted. This method shows high potential for future research, especially in times of climate change, where the assessment of ecosystem functioning will gain further importance in order to sustainably manage marine ecosystems.

2. Material and Methods

2.1. Study Area

The Barents Sea is an open arcto-boreal sea which lies entirely north of the Arctic Circle. It is one of the deepest shelf seas surrounding the Arctic Ocean. Its depth ranges between 20 and 500 meters, with an average depth of 230 meters (Loeng, 1991). The Barents Sea is located on the western part of the Eurasian shelf, with a total area of about 1 400 000 km², extending from 66.7°N to 82.5°N and from 8.0°E to 68.5°E. The Barents Sea western boundary lies at the continental break west of Norway and west Spitsbergen, while the shelf break north of Svalbard and Franz Josef Land archipelago defines the northern boundary. To the east, it can be distinguished from the Kara Sea from Cape Kanin at the northwestern tip of the Kanin Peninsula, to Cape Svyatoy on the Kola Peninsula (see Fig. 1) (Jakobsen & Ozhigin, 2011).

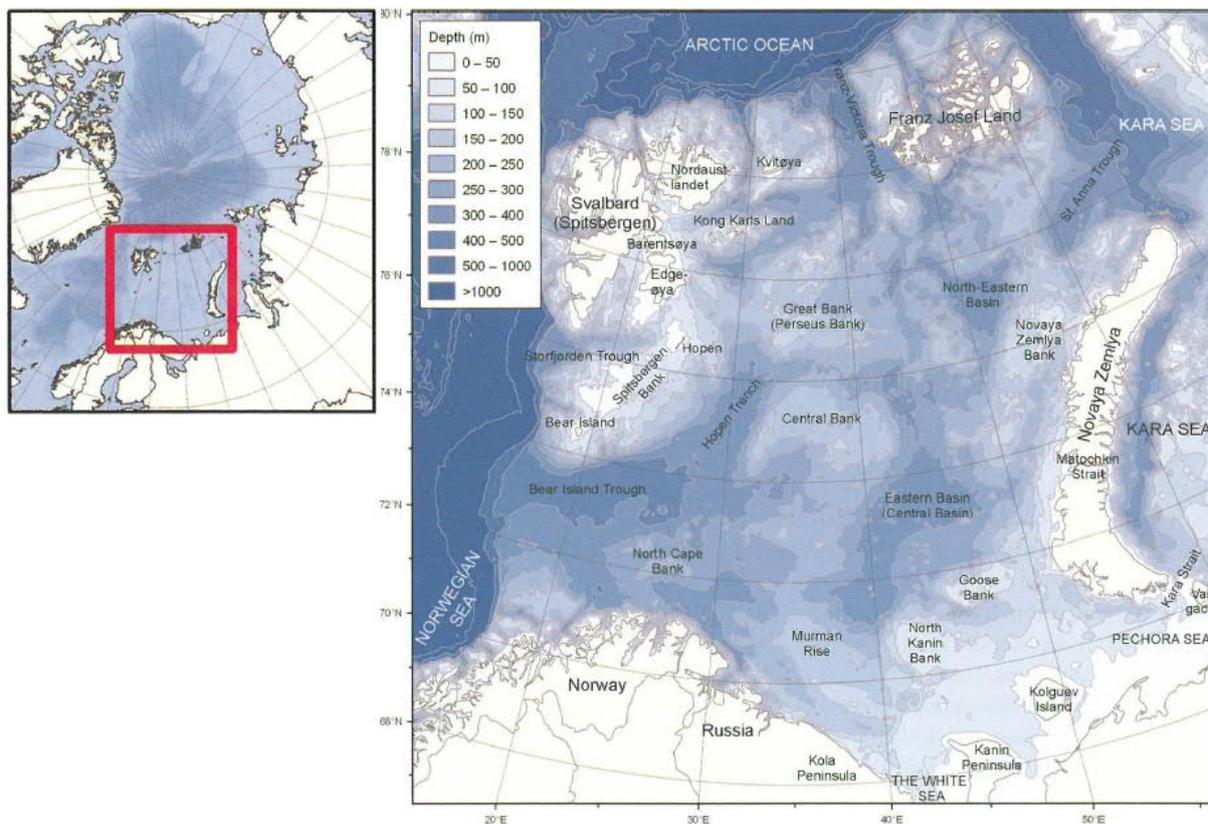


Fig. 1: The Barents Sea. Large map with bottom topography and geographical names. Image adapted from Jakobsen and Ozhigin (2011).

The circulation within the Barents Sea is rather complicated and variable, as it is influenced by various factors such as bottom topography and water inflow from adjacent seas. The Barents Sea is often considered a pathway and transition zone between the Atlantic and Arctic Ocean, as Atlantic water passes through, entering the Arctic. Warm and saline waters enter on their way from the Atlantic to Arctic, whereas cold and less saline waters traverse through the Barents Sea from the Arctic to the Atlantic Ocean (Jakobsen & Ozhigin, 2011). The Barents Sea is therefore characterized by three main water masses: Coastal, Atlantic, and Arctic (Jakobsen & Ozhigin, 2011). The same categorization applies for the three Currents of the Barents Sea: (1) The Norwegian Coastal Current runs along the western and northern coast of Norway. (2) The Atlantic current is found in the south and is mainly directed towards the east. (3) The direction of the Arctic current in the north of the Barents Sea is directed towards the west and southwest (Loeng, 1991). The transition area between the warm and saltier Atlantic water and the colder and fresher Arctic water in the Barents Sea is known as the polar front (Jakobsen & Ozhigin, 2011). The polar front was believed to have a fixed position at 250m isobath (e.g. Gawarkiewicz & Plueddemann, 1995) but was then found to be not stationary. Ingvaldsen (2005) showed that the location of the polar front varies in phase with the climate of the Barents Sea, where it moves further upslope in warmer periods with stronger winds.

The transport of cold and warm water masses as well as solar radiation and atmospheric circulation, affect the air temperature in the Barents Sea. In January, temperatures range from -25°C in the north to -7°C in the south and from 1°C to 12°C in July. Besides, current patterns of the Barents Sea also influence its water temperature. The temperature of Barents Sea waters remains positive throughout the year in the southwestern and central parts. Though there is a general decrease in temperature from west to east and from south to north, caused by currents. Hence, the northern parts of the Barents Sea are generally colder, with a cold intermediate layer with temperatures below -1°C (Jakobsen & Ozhigin, 2011).

Parts of the Barents Sea also feature an extensive permanent and seasonal ice cover, though there is a high seasonality in the extent of the ice as it is influenced by both the Atlantic and the Arctic Oceans, as well as by atmospheric conditions. In winter, the Arctic water is usually covered with ice, where the marginal ice zone reaches the polar front (Slagstad & McClimans, 2005). In cold years, the eastern and southeastern Barents Sea is also covered with ice during winter. During relatively warm years the northern Barents Sea will be ice-covered during winter only, but not in

summer. In general, the seasonal cycle and inter-annual variability of the sea ice coverage is quite large in the Barents Sea, dependent whether the winter is mild or severe. The maximum ice coverage typically occurs in the months of March and April (Jakobsen & Ozhigin, 2011).

The Barents Sea is one of the most productive seas adjacent to the Arctic as well as among the most productive fisheries in the world (Eide & Heen, 2002). The Barents Sea serves as an important nursing area and presently contains the largest existing population of Atlantic cod *Gadus morhua* (Linnaeus, 1758) in the North Atlantic (Gjørseter, 2009). Additional species with commercial interest found in the Barents Sea are: Capelin *Mallotus villosus* (Müller, 1776), Atlantic Herring *Clupea harengus* (Linnaeus, 1758), Haddock *Melanogrammus aeglefinus* (Linnaeus, 1758), Saithe *Pollachius virens* (Linnaeus, 1758), Redfish *Sebastes* sp., Greenland halibut *Reinhardtius hippoglossoides* (Walbaum, 1792), Polar cod *Boreogadus saida* (Lepechin, 1774), Wolffish *Anarhichas* sp., Long rough dab *Hippoglossoides platessoides* (Fabricius, 1780), European Plaice *Pleuronectes platessa* (Linnaeus, 1758), and Blue whiting *Micromesistius poutassou* (Risso, 1827) (Fossheim et al., 2006; Hamre, 1994; Jakobsen & Ozhigin, 2011). The annual yields of fish in the Barents Sea vary between 0.5 and 4.5 million tons and fishing pressure is generally high (Nakken, 1998). Besides, many non-commercial fish species exist, as it is known that around 200 different fish from 66 families occur in the Barents Sea, of which around 100 species are commonly observed (Fossheim et al., 2006; Wiedmann et al., 2014). It is also a system with relatively low biodiversity, but a very high degree of species interaction (Wassmann et al., 2006).

2.2. Fish species

For this study, images of the most commonly observed fish species of the Barents Sea were collected and analyzed. Table 1 shows a list of the Barents Sea fish species as adapted from Wiedmann et al. (2014). Authors and common names were adapted from the World Register of Marine Species (WoRMS, 2014) and the Atlas of the Barents Sea fishes (Wienerroither, 2011). The ecological information on habitat, biogeography and diet are also listed in Table 1 as adapted from Wiedmann et al. (2014).

Table 1: List of most commonly observed fish species of the Barents Sea including Latin abbreviations (Abb.) and information on habitat, biogeography and diet. **Dem:** Demersal; **Pel:** Pelagic; **A:** Arctic; **B:** Boreal; **AB:** Arcto-Boreal; **Ben:** Benthosfeeder; **B/I:** Benthos/Ichthyophage; **Ich:** Ichthyophage; **P/I:** Plankton/Ichthyophage; **Ich:** Ichthyophage.

#	Species names	Abb.	Common Name	Habitat	Biogeog.	Diet
-	<i>Amblyraja hyperborea</i> (Collett, 1879)	Am_hy	Arctic skate	-	-	-
-	<i>Amblyraja radiata</i> (Donovan, 1808)	Am_ra	Thorny skate	-	-	-
1	<i>Anarhichas denticulatus</i> (Krøyer, 1845)	An_de	Northern wolffish	Dem	B	Ben
2	<i>Anarhichas lupus</i> (Linnaeus, 1758)	An_lu	Atlantic wolffish	Dem	B	Ben
3	<i>Anarhichas minor</i> (Olafsen, 1772)	An_mi	Spotted wolffish	Dem	B	Ben
4	<i>Anisarchus medius</i> (Reinhardt, 1837)	An_me	Stout eelblenny	Dem	B	Ben
5	<i>Arctogadus glacialis</i> (Peters, 1872)	Ar_gl	Arctic cod	Pel	A	Pla
6	<i>Arctozenus risso</i> (Bonaparte, 1840)	Ar_ri	Spotted barracudina	Pel	B	Pla
7	<i>Argentina silus</i> (Ascanius, 1775)	Ar_si	Greater argentine	Pel	B	Pla
8	<i>Artediellus atlanticus</i> (Jordan & Evermann, 1898)	Ar_at	Atlantic hookear sculpin	Dem	B	Ben
-	<i>Bathyraja spinicauda</i> (Jensen, 1914)	Ba_sp	Spinytail skate	-	-	-
9	<i>Bentosema glaciale</i> (Reinhardt, 1837)	Be_gl	Glacier lanternfish	Pel	B	Pla
10	<i>Boreogadus saida</i> (Lepechin, 1774)	Bo_sa	Polar cod	Pel	A	Pla

11	<i>Brosme brosme</i> (Ascanius, 1772)	Br_br	Tusk	Dem	B	Ben
12	<i>Careproctus</i> sp. (Krøyer, 1861)	Ca_re	-	Dem	A	Ben
13	<i>Chimaera monstrosa</i> (Linnaeus, 1758)	Ch_mo	Rabbit-fish	Dem	B	Ben
14	<i>Clupea harengus</i> (Linnaeus, 1758)	Cl_ha	Atlantic herring	Pel	B	Pla
15	<i>Cottunculus sadko</i> (Essipov, 1937)	Co_sa	Sadko sculpin	Dem	A	Ben
16	<i>Cyclopterus lumpus</i> (Linnaeus, 1758)	Cy_lu	Lumpsucker	Dem	B	Pla
17	<i>Enchelyopus cimbrius</i> (Linnaeus, 1766)	En_ci	Fourbeard rockling	Dem	B	Ben
18	<i>Entelurus aequoreus</i> (Linnaeus, 1758)	En_ae	Snake pipefish	Pel	B	Pla
19	<i>Eumicrotremus derjugini</i> (Popov, 1926)	Eu_de	Leatherfin lumpsucker	Dem	A	Pla
20	<i>Eumicrotremus spinosus</i> (Fabricius, 1776)	Eu_sp	Atlantic spiny lumpsucker	Dem	A	Pla
21	<i>Gadiculus argenteus</i> (Guichenot, 1850)	Ga_ar	Silvery pout	Pel	B	Pla
22	<i>Gadus morhua</i> (Linnaeus, 1758)	Ga_mo	Atlantic cod	Dem	B	Ich
23	<i>Gaidropsarus argentatus</i> (Reinhardt, 1837)	Ga_ar	Arctic rockling	Dem	A	B/I
24	<i>Gasterosteus aculeatus</i> (Linnaeus, 1758)	Ga_ac	Three-spined stickleback	Pel	B	Pla
25	<i>Glyptocephalus cynoglossus</i> (Linnaeus, 1758)	Gl_cy	Witch flounder	Dem	B	Ben
26	<i>Gymnelus</i> sp. (Reinhardt, 1833)	Gy_sp	-	Dem	A	Ben
27	<i>Gymnocanthus tricuspis</i> (Reinhardt, 1830)	Gy_tr	Arctic staghorn sculpin	Dem	A	Ben
28	<i>Hippoglossoides platessoides</i> (Fabricius, 1780)	Hi_pl	Long rough dab	Dem	B	B/I
29	<i>Hippoglossus hippoglossus</i> (Linnaeus, 1758)	Hi_hi	Atlantic halibut	Dem	B	Ich

30	<i>Icelus bicornis</i> (Reinhardt, 1840)	Tr_bi	Two-horn sculpin	Dem	A	Ben
31	<i>Icelus spatula</i> (Gilbert & Burke, 1912)	Ic_sp	Spatulate sculpin	Dem	AB	Ben
32	<i>Leptagonus decagonus</i> (Bloch & Schneider, 1801)	Le_de	Atlantic poacher	Dem	AB	Ben
33	<i>Leptoclinus maculatus</i> (Fries, 1838)	Le_ma	Daubed shanny	Dem	B	Ben
34	<i>Limanda limanda</i> (Linnaeus, 1758)	Li_li	Common dab	Dem	B	Ben
35	<i>Liparis fabricii</i> (Krøyer, 1847)	Li_fa	Gelatinous snailfish	Dem	A	Pla
36	<i>Liparis gibbus</i> (Bean, 1881)	Li_ba	Variegated snailfish	Dem	A	B/I
37	<i>Lumpenus fabricii</i> (Reinhardt, 1836)	Lu_fa	Slender eelblenny	Dem	A	Ben
38	<i>Lumpenus lampraeformis</i> (Walbaum, 1792)	Lu_la	Snakeblenny	Dem	B	Ben
39	<i>Lycenchelys kolthoffi</i> (Jensen, 1904)	Ly_ko	Checkered wolf eel	Dem	A	Ben
40	<i>Lycodes esmarkii</i> (Collett, 1875)	Ly_es	Greater eelpout	Dem	B	Ben
41	<i>Lycodes eudipleurostictus</i> (Jensen, 1902)	Ly_eu	Doubleline eelpout	Dem	A	Ben
42	<i>Lycodes frigidus</i> (Collett, 1879)	Ly_fr	Glacial eelpout	Dem	A	Ben
43	<i>Lycodes gracilis</i> (Sars, 1867)	Ly_gr	Vahl's eelpout	Dem	B	Ben
44	<i>Lycodes pallidus</i> (Collett, 1879)	Ly_pa	Pale eelpout	Dem	A	Ben
45	<i>Lycodes polaris</i> (Sabine, 1824)	Ly_po	Canadian eelpout	Dem	A	Ben
46	<i>Lycodes reticulatus</i> (Reinhardt, 1835)	Ly_re	Arctic eelpout	Dem	A	B/I
47	<i>Lycodes rossi</i> (Malmgren, 1865)	Ly_ro	Threespot eelpout	Dem	A	Ben
48	<i>Lycodes seminudus</i> (Reinhardt, 1837)	Ly_se	Longear eelpout	Dem	A	B/I
49	<i>Lycodes squamiventer</i> (Jensen, 1904)	Ly_sq	Scalebelly eelpout	Dem	A	Ben

50	<i>Lycodonus flagellicauda</i> (Jensen, 1902)	Ly_fl	-	Dem	A	Ben
51	<i>Macrourus berglax</i> (Lacepède, 1801)	Ma_be	Roughhead grenadier	Dem	B	Ben
52	<i>Mallotus villosus</i> (Müller, 1776)	Ma_vi	Capelin	Pel	B	Pla
53	<i>Maurolicus muelleri</i> (Gmelin, 1789)	Ma_mu	Silvery lightfish	Pel	B	Pla
54	<i>Melanogrammus aeglefinus</i> (Linnaeus, 1758)	Me_ae	Haddock	Dem	B	Ben
55	<i>Merlangius merlangus</i> (Linnaeus, 1758)	Me_me	Whiting	Dem	B	Ich
56	<i>Micromesistius poutassou</i> (Risso, 1827)	Mi_po	Blue whiting	Pel	B	P/I
57	<i>Microstomus kitt</i> (Walbaum, 1792)	Mi_ki	Lemon sole	Dem	B	Ben
58	<i>Molva molva</i> (Linnaeus, 1758)	Mo_mo	Ling	Dem	B	Ich
59	<i>Myoxocephalus scorpius</i> (Linnaeus, 1758)	My_sc	Shorthorn sculpin	Dem	B	B/I
60	<i>Paraliparis bathybius</i> (Collett, 1879)	Pa_ba	Black seasnail	Dem	A	Pla
61	<i>Pleuronectes platessa</i> (Linnaeus, 1758)	Pl_pl	European plaice	Dem	B	Ben
62	<i>Pollachius virens</i> (Linnaeus, 1758)	Po_vi	Saithe	Pel	B	P/I
-	<i>Rajella fyllae</i> (Lütken, 1887)	Ra_fy	Round skate	-	-	-
63	<i>Reinhardtius hippoglossoides</i> (Walbaum, 1792)	Re_hi	Greenland halibut	Dem	B	Ich
64	<i>Sebastes mentella</i> (Travin, 1951)	Se_me	Beaked redfish	Dem	B	P/I
65	<i>Sebastes norvegicus</i> (Ascanius, 1772)	Se_no	Golden redfish	Dem	B	P/I
66	<i>Sebastes viviparus</i> (Krøyer, 1845)	Se_vi	Norway redfish	Dem	B	Ben
67	<i>Sommiosus microcephalus</i> (Bloch & Schneider, 1801)	So_mi	Greenland shark	Dem	B	Ich

68	<i>Triglops murrayi</i> (Günther, 1888)	Tr_mu	Moustache sculpin	Dem	B	Ben
69	<i>Triglops nybelini</i> (Jensen, 1944)	Tr_ny	Bigeye sculpin	Dem	A	Pla
70	<i>Triglops pingelii</i> (Reinhardt, 1837)	Tr_pi	Ribbed sculpin	Dem	AB	Ben
71	<i>Trisopterus esmarkii</i> (Nilsson, 1855)	Tr_es	Norway pout	Pel	B	Pla
72	<i>Ulcina olrikii</i> (Lütken, 1877)	Ul_ol	Arctic alligatorfish	Dem	A	Ben

2.3. Survey

A boat survey was conducted from the 27th of January to the 31st of January 2014 within the Balsfjord in Northern Norway (see Fig. 2) to sample fish and take pictures of the different species.



Fig. 2: Map of the Balsfjord in Northern Norway, south of Tromsø. Image by Google earth.

The vessel ‘Johan Ruud’ (Fig. 3) was used to conduct the survey, which is a multi-purpose stern trawler, owned by the Norwegian Government and managed by the Norwegian College of Fishery Science (University of Tromsø). The ‘Johan Ruud’ was built in 1976 at Sterkoder



Fig. 3: Photo of the vessel 'Johan Ruud'. Image from uit.no.

Mekaniske Verksted Ltd., Kristiansund (Norway) and is 30.50 meters long with a maximum speed of 10 knots (www.uit.no). A small scale shrimp trawl net with a cover and a codend was used during the survey. The net included a grid installation and alternatively a square mesh panel that led 'escaping fish' into the cover. The survey was conducted as part of a research project for the Master thesis of Ixai Salvo Borda. A total of 22 hauls were conducted during the study period. The exact coordinates of the area trawled, and the trawling time and depth can be found in Table 2.

Table 2: Trawling details of the survey in the Balsfjord.

Date	Haul No.	Start Time	Finish Time	Position - Start	Position - Finish	Depth - Start [m]	Depth - Finish [m]	Trawling time [min]	Speed	State	Selective device
27.01.2014	1	12:40	13:01	69°22'2"N - 19°03'8"E	69°21'6"N - 19°04'8"E	188	186	21	14	Valid	Grid
27.01.2014	2	15:14	15:36	69°22'3"N - 19°04'2"E	69°21'6"N - 19°05'3"E	186	184	21	15	Invalid	Grid
27.01.2014	3	16:58	17:18	69°22'1"N - 19°04'8"E	69°21'5"N - 19°05'2"E	187	185	20	14	Valid	Grid
28.01.2014	4	08:40	09:00	69°22'1"N - 19°04'3"E	69°21'5"N - 19°05'3"E	187	186	20	14	Valid	Grid
28.01.2014	5	10:00	10:21	69°21'9"N - 19°04'7"E	69°21'3"N - 19°05'8"E	187	184	21	16	Valid	Grid
28.01.2014	6	11:56	12:16	69°19'8"N - 19°22'1"E	69°19'2"N - 19°22'7"E	126	123	20	12	Valid	Grid
28.01.2014	7	12:55	13:15	69°19'9"N - 19°21'7"E	69°19'3"N - 19°22'5"E	126	123	20	10	Valid	Grid
28.01.2014	8	14:50	15:11	69°19'8"N - 19°21'9"E	69°19'2"N - 19°22'6"E	126	122	21	7	Valid	Grid
29.01.2014	9	08:35	08:55	69°19'5"N - 19°22'2"E	69°20'1"N - 19°21'7"E	124	126	20	5	Valid	Grid
29.01.2014	10	09:22	09:42	69°20'0"N - 19°21'7"E	69°19'4"N - 19°22'5"E	127	124	20	6	Valid	Grid
29.01.2014	11	10:27	10:47	69°19'5"N - 19°22'2"E	69°20'2"N - 19°21'5"E	125	127	20	6	Valid	Grid
29.01.2014	12	11:47	12:07	69°21'8"N - 19°05'2"E	69°22'6"N - 19°03'7"E	185	190	20	7	Valid	Grid
29.01.2014	13	12:43	13:03	69°22'2"N - 19°04'2"E	69°21'6"N - 19°05'4"E	188	187	20	8	Valid	Grid
29.01.2014	14	13:36	14:00	69°22'0"N - 19°04'5"E	69°22'5"N - 19°03'3"E	187	188	24	7	Valid	Grid
30.01.2014	15	08:51	09:01	69°22'0"N - 19°04'3"E	69°21'8"N - 19°04'9"E	187	186	10	7	Invalid	Square Mesh Panel
30.01.2014	16	10:36	10:56	69°21'8"N - 19°04'8"E	69°21'4"N - 19°06'3"E	187	185	20	6	Valid	Square Mesh Panel
30.01.2014	17	11:41	12:01	69°21'9"N - 19°04'6"E	69°21'4"N - 19°06'1"E	188	186	20	7	Valid	Square Mesh Panel
30.01.2014	18	13:18	13:38	69°19'9"N - 19°21'8"E	69°19'3"N - 19°22'4"E	127	125	20	6	Valid	Square Mesh Panel
30.01.2014	19	14:22	14:42	69°19'6"N - 19°22'2"E	69°20'30"N - 19°21'5"E	125	126	20	4	Valid	Square Mesh Panel
31.01.2014	20	08:38	08:58	69°19'6"N - 19°22'3"E	69°20'2"N - 19°21'5"E	123	125	20	4	Valid	Square Mesh Panel
31.01.2014	21	09:48	10:09	69°19'9"N - 19°21'7"E	69°19'3"N - 19°22'6"E	126	123	21	6	Valid	Square Mesh Panel
31.01.2014	22	10:38	10:58	69°19'6"N - 19°22'3"E	69°20'2"N - 19°21'7"E	124	126	20	7	Valid	Square Mesh Panel

2.4. Picture collection

During the survey, a total of 11 different fish species were photographed with a Nikon D200 mounted on a Kaiser Repro Camera Stand. The camera was screwed on to the pole of the stand on which it could be adjusted in height. The fish were placed individually on to the board below with a scaling grid, where two lamps were mounted on to and adjusted accordingly for

sufficient light supply. A plastic foil was wrapped around the board to avoid damage and dirt. The equipment and the camera setup can be seen in Figure 4.

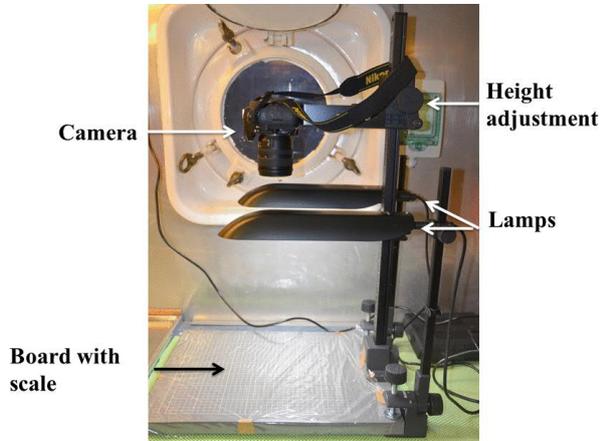


Fig. 4: Camera setup with which the pictures of the sampled fish were taken during the survey.

All species caught during the survey were identified on board via identification keys and then photographed from their left side with the according name tags, to ensure that images and species could be identified later during the picture analysis. The (for this study relevant) species which were sampled and photographed during the boat survey can be found in Table 3.

Table 3: Species sampled during the boat survey.

Species
<i>Anarhichas lupus</i>
<i>Clupea harengus</i>
<i>Cyclopterus lumpus</i>
<i>Gadus morhua</i>
<i>Glyptocephalus cynoglossus</i>
<i>Hippoglossoides platessoides</i>
<i>Leptagonus decagonus</i>
<i>Melanogrammus aeglefinus</i>
<i>Micromesistius poutassou</i>
<i>Microstomus kitt</i>
<i>Pleuronectes platessa</i>

For those species of the Barents Sea that could not be sampled during the survey, alternative sources were used to collect images and drawings of the fish. Posters with fish drawings were ordered online from the Scandinavian Fishing Year Book at www.scandfish.com. The fish drawings were scanned and digitalized individually and saved as jpeg-files. Species images which were neither photographed during the survey nor included on the scandfish-poster were either taken out of the pdf version of the 'Atlas of the Barents Sea Fishes' (Wienerroither, 2011), or from the websites World Register of Marine Species (WoRMS, 2014) and www.species-identification.org. The images were obtained via screenshots with the program 'Snipping tool' and saved as jpeg-files. The image acknowledgements, the type of image (drawing or photograph) and the source can be found in the Appendix (App. 1). All used images show the fish from its left side.

2.5. Landmarks

The currently available literature was scanned for previous work on landmarks (LM) on fish which included publications from several authors, namely: Clabaut, Bunje, Salzburger, and Meyer (2007); Fink and Zelditch (1995); A. Loy et al. (2000); Angelo Loy, Busilacchi, Costa, Ferlin, and Cataudella (2000); Angelo Loy et al. (1998); Park et al. (2013); Rüber and Adams (2001); Russo et al. (2012); Sarà et al. (1999). The landmarks were then chosen according to what was available in the literature and which ones seemed to be the most common choices among publications. Functional aspects of the morphology were also taken into consideration when deciding on which landmarks to use.

Table 4 shows the list of the landmarks which were chosen for this study. The landmarks were chosen originally to fit fish species with 3 dorsal fins and 2 anal fins. However, several species in this study differ anatomically and e.g. will only show two or one dorsal fin. In such cases, still all landmarks were set to be consistent throughout the LM-setting process. But to be able to distinguish redundant landmarks from precise ones later on during analysis, a rating system was used. All landmarks were rated from 1 to 3, according to their precision and the certainty with which they were set. Landmarks that left no doubts about their correctness were rated as '1', the ones that involved small uncertainty as '2' and landmarks that were either redundant or set with very high uncertainty were rated as '3'.

The flat fish species posed some extra difficulties as they show two eyes from the dorsal view. For those species, the “lower left” eye (left as from posterior to anterior view) was chosen for landmark one, the center of the eye.

Four out of the 76 species were not provided with landmarks as those four species are skates which were anatomically too different to include them in this landmark-based study. The excluded four species are: *Amblyraja hyperborea*, *Amblyraja radiata*, *Bathyraja spinicauda* and *Rajella fyllae*.

Table 4: List of landmarks that were set with the anatomical description of the landmark location.

Order	Land mark	Description		
		3 dorsal fins - 2 anal fins	2 dorsal fins - 1 anal fin	1 dorsal fin
1	LM1	Center of the eye		
2	LM2	Posterior corner of the mouth		
3	LM3	Anterior tip of snout at upper jaw		
4	LM4	top of the operculum that shows the end position of the head on dorsal midline		
5	LM5	Anterior insertion of first dorsal fin	Anterior insertion of the anterior dorsal fin	Anterior insertion of the dorsal fin
6	LM6	Anterior insertion of second dorsal fin	Anterior insertion of the posterior dorsal fin	Midpoint of the dorsal fin on dorsal midline
7	LM7	anterior insertion of third dorsal fin	Anterior insertion of the posterior dorsal fin	midpoint of the dorsal fin on dorsal midline
8	LM8	posterior insertion of third dorsal fin	Posterior insertion of the posterior dorsal fin	posterior insertion of dorsal fin
9	LM9	maximum dorsal curvature of the dorsal peduncle		
10	LM10	ventral insertion of caudal fin		
11	LM11	dorsal insertion of the caudal fin		
12	LM12	Posterior-most tip of the caudal peduncle at the lateral midline		
13	LM13	maximum ventral curvature of the ventral peduncle		
14	LM14	posterior insertion of posterior-most anal fin	posterior insertion of the anal fin	
15	LM15	anterior insertion of posterior-most anal fin	midpoint of the anal fin on ventral midline	
16	LM16	anterior insertion of anterior anal fin	anterior insertion of the anal fin	

17	LM17	dorsal-anterior insertion of the pelvic fin
18	LM18	Insertion of the operculum at the ventral midline
19	LM19	upper-anterior base/insertion of the pectoral fin

The image processing and analysis program ImageJ was downloaded for Windows at <http://imagej.nih.gov/ij/> and installed. The jpeg-images of the different fish were opened with ImageJ and the landmarks were set via the multi-point tool function and then saved as XY-coordinates in a text file. The images with the set landmarks were also saved in a Tiff-format. Figure 5 shows an example of an image of *Gardiculus argenteus* with the according landmarks (in blue) that were set in ImageJ. All XY-coordinates of the two-dimensional set of 19 landmarks were then copied from the text file into an excel sheet, which also included species name, number of dorsal and anal fins, and the rating of each landmark.

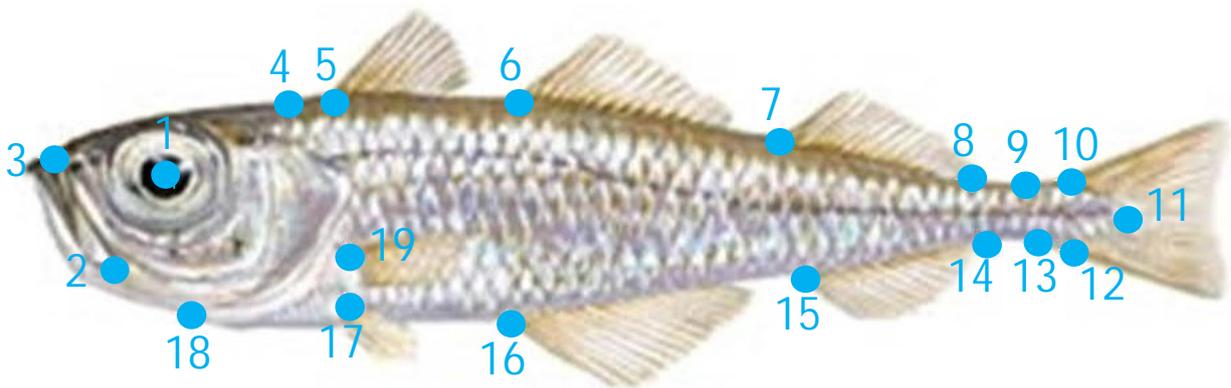


Fig. 5: *Gardiculus argenteus* with landmarks 1-19 (in blue) that were set with the program ImageJ.

2.6. Statistical Analysis

The statistical analysis was conducted with the statistical computing program R which can be downloaded and installed for free from the Comprehensive R Archive Network, CRAN. The working package geomorph was used to perform the geometric morphometric shape analysis (D. Adams & Otárola-Castillo, 2012; D. C. Adams & Otárola-Castillo, 2013). The digitized landmarks were read into R from the excel file and stored as a two-dimensional array for subsequent analysis. To superimpose all species to a common coordinate system while holding constant variation in their position, size, and orientation, a Generalized Procrustes Analysis (GPA) was performed (D. C. Adams & Otárola-Castillo, 2013). Then a Principal

Component Analysis (PCA) of the shape data was conducted and the results were presented graphically. As many landmarks were rated as '3' (see Table 5), 6 different datasets were created for which the principal component analysis was carried out. For each dataset different landmarks were removed, according to their rating, to reduce the level of uncertainty. The datasets can be found in Table 6.

Dataset #5 was chosen for all further analysis, as it showed the highest Principle Component values while containing the most landmarks. All other datasets were disregarded.

Table 5: Number of times each landmark was rated as '3' for the whole dataset. Non-listed LMs were never rated with '3'.

Landmark	LM 7	LM 9	LM1 3	LM1 4	LM 8	LM1 0	LM1 2	LM1 7	LM1 5	LM1 8	LM1 6	LM1 9
Times rated '3'	60	22	22	20	19	19	19	18	4	2	1	1

Table 6: Overview of the 6 different datasets that were created and selected for statistical analysis.

Dataset	Landmarks removed	Total Number of Landmarks
Set # 1	None	19
Set # 2	LM7	18
Set # 3	LM7, LM 9, LM13	16
Set # 4	LM7, LM 9, LM13, LM8, LM14	14
Set # 5	LM7, LM 9, LM13, LM10, LM12	14
Set # 6	LM7, LM 9, LM13, LM10, LM12, LM8, LM14, LM17	11

Then a table was created in Excel with the Principal Components (PC) 1 through 5 for each species and information on the environmental variables 'Diet', 'Habitat', and 'Biogeography' were added, made available through Magnus Aune Wiedmann (Wiedmann et al., 2014). The variable 'Diet' was split into 5 categories: (1) Benthosfeeder; (2) Benthos/Ichthyophage; (3) Ichthyophage; (4) Plankton/Ichthyophage; and (5) Planktonfeeder. 'Habitat' consisted of the two categories (1) demersal and (2) pelagic; where 'demersal' summarized bottom and epibenthic-pelagic habitats and 'pelagic' the nerito-pelagic, bathypelagic and cryopelagic habitats.

‘Biogeography’ was classified as (1) arctic; (2) arcto-boreal; and (3) boreal. The according environmental information for each species can be found in Table 1 (see above).

The first five Principal components and their corresponding deformation grids were plotted in tangent space for the 72 fish species. In the PC-plots the species were color-coded according to their biogeographical affiliation.

As a next step, analysis of variance (ANOVA) was performed for all five shape axis in relation to the three environmental factors diet, habitat and biogeography. The ANOVA was performed in order to detect possible associations of the five PC shape-axes with any environmental factors. Therefore, each of the five principal components were tested for significant differences with regard to each environmental variable. Interactions between biogeography and habitat as well as between biogeography and diet were tested. For the interaction-testing between biogeography and diet, the Arcto-Boreal species were excluded because the Arcto-Boreal group consisted of three species only and contained nothing but Benthosfeeding fish. This did not allow for a comparison between different diets in Arcto-Boreal fish. Arcto-Boreal species were also removed from the analysis of interaction between biogeography and habitat. In this scenario Arcto-Boreal species again presented only one group, as all three species are demersal.

Additionally, a redundancy analysis was performed. The different shape axes PC1 through PC5 were analyzed with regard to the variables biogeography and diet, as well as biogeography and habitat. In order to also visually detect patterns of correlation between the variables and to find similarities between the species, biplots of the RDA were created. The species were plotted along the first to RDA axes (RDA1 and RDA2), color-coded according to their biogeographical association and the centroids for the PC-axis were added.

A map of the Barents Sea was created in R. To show each fish’s distribution centroid, the fish species were plotted in the map at their mean mass center of gravity. The distribution centroids were obtained from the Joint Russian-Norwegian ecosystem survey (for details see Wienerroither, 2011). Distribution centroids were available for 67 of the 72 species but due to the lack of data, five species *Benthosema glaciale*, *Gymnelus* sp., *Lycenchelys kolthoffi*, *Paraliparis bathybius* and *Ulcina olrikii* were not included in the map. The species were plotted as small shape icons at their distribution centroids. The shapes were obtained by using the points of the Procrustes aligned landmarks for each species, connecting them with lines and filling in

the shapes with color. The names of each species were added to the plot, using the Latin abbreviations for each fish (as listed in Table 1).

The additional R packages ‘geomorph’, ‘car’, ‘vegan’, ‘gstat’, ‘maptools’, ‘rgdal’, ‘splancs’, and ‘fields’ were used for the statistical analyses.

3. Results

3.1. Principal Component Analysis (PCA)

In the PCA representation of total shape variation, the first principal component PC1 explained 39.7% of total shape variation, the second 21.1% and the first five principal components together explained a cumulative 86.4% of shape variation (see Table 7). It has to be highlighted here, that the first two Principle Components are of much higher importance. Both PC1 and PC2 explain most of the variation in the dataset, PC3 with 12.3% is of small importance and PC4 and PC5 explain very little shape variation with only 6.28% (Table 7). All principle components will be treated within the results section for the sake of completeness. In the discussion, the main focus will be put on the first two principle components as they explain the most shape variation within the data.

Table 7: First five Principle Component (PC) scores for all 72 fish species.

	PC1	PC2	PC3	PC4	PC5
Standard Deviation	0.1355	0.09883	0.07533	0.05683	0.05390
Proportion of Variance	0.3974	0.21141	0.12280	0.06990	0.06288
Cumulative Proportion	0.3974	0.60877	0.73157	0.80147	0.86435

The shape axis PC1 explains a shape deformation on the head and posterior of the fish, as well as on the position of dorsal and anal fins, on how they are distributed along the dorsal and lateral midline and/or whether they are short- or long-based (Fig. 6). Species with negative PC1-values on the left side have shorter and smaller heads, and long-based dorsal and anal fins reaching to the far back, close to the caudal fin, as for example in the witch flounder (*Glyptocephalus cynoglossus*). Species with positive PC1-values on the right side of the plot in Fig. 6 show a constriction within the posterior in the deformation grid, where the dorsal and anal fins are short-based and located further towards the caudal fin as represented by the lumpsucker (*Cyclopterus lumpus*). Arctic species show mostly negative PC1 values and are clustering in the lower left with negative PC1 and PC2 values, such as the European plaice *Pleuronectes platessa* (60), *Lycodon flagellicauda* (50), snakeplenny *Lumpenus lampretaeformis* (38), checkered wolf eel *Lycenchelys kolthoffi* (39), glacial eelpout *Lycodes frigidus* (42) and Threespot eelpout *Lycodes rossi* (47). This cluster consists of demersal species only.

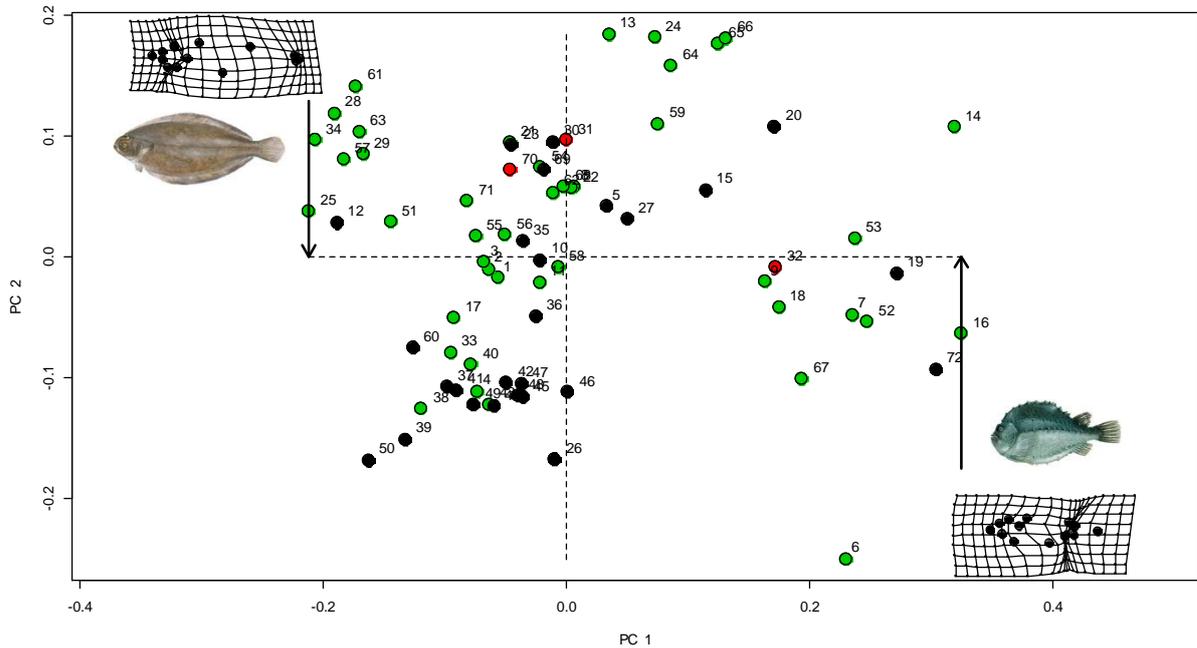


Fig. 6: Tangent space plot of species along the principal axes one and two (PC1 & PC2) with deformation grids of PC1. Fish images represent species with highest positive (on the right) and negative (on the left) PC1 values. Numbers represent species as listed in Table 1. **Black dots:** Arctic species; **green dots:** Boreal species; **red dots:** Arcto-Boreal species; **fish images:** left: *Glyptocephalus cynoglossus*, witch flounder (25); right: *Cyclopterus lumpus*, lumpfish (16).

Negative values of shape axis PC2 represent an elongated, eel-like body shape, as shown in the deformation grids in Fig. 7. Hence, the cluster of the Arctic species in the lower left of Fig. 6 consists of specimens with short heads, long-based dorsal and caudal fins and eel-like bodies.

Boreal species show both, negative and positive PC1-values, though the majority lies on the left side of the plot in Fig. 6. A small cluster of Boreal species is present in the upper left side of the plot, containing demersal species only, e.g. European plaice *Pleuronectes platessa* (61), long rough dab *Hippoglossoides platessoides* (28), Greenland halibut *Reinhardtius hippoglossoides* (63), common dab *Limanda limanda* (34), Atlantic halibut *Hippoglossus hippoglossus* (29) and others (see Fig. 6). Interestingly, all boreal species within this cluster are flatfish.

Within the center of the plot in Fig. 6 lies a mixed cluster of Boreal and Arctic species. It consists, besides others, of the five pelagic species: Atlantic cod *Gadus morhua*, Arctic cod *Arctogadus glacialis* (5), blue whiting *Micromesistius poutassou* (56), haddock *Melanogrammus aeglefinus* (54) and polar cod *Boreogadus saida* (10). These show slightly elongated body shapes and evenly distributed dorsal fins along the dorsal midline.

In the upper right in Fig. 6, a small, less dense cluster of arctic and boreal species on the positive side of PC1 and PC2 is present. It consists of one pelagic species, the three-spined stickleback *Gasterosteus aculeatus* (24) and otherwise demersal species only, such as the three Redfish (64-66), the shorthorn sculpin *Myoxocephalus scorpius* (59) and others (see Fig.6). These species present relatively large heads, wide-based dorsal fins and slightly elongated body shapes.

Towards the far right within the positive side of PC1, both Arctic and Boreal, as well as demersal and pelagic species are found. Demersal species like the Atlantic herring *Clupea harengus* (14) and the Capelin *Mallotus villosus* (52) are present. Examples of demersal species within this cluster are the Greenland shark *Somniosus microcephalus* (67) and the leatherfin lump sucker *Eumicrotremus derjugini* (19) (Fig. 6). Such species represent slightly elongated body shapes and short-based dorsal and anal fins.

The three Arcto-Boreal species do not show any clustering and present negative and positive PC1-values (Fig. 6). The two most extreme shapes of PC1 are represented by species 25, *Glyptocephalus cynoglossus*, the witch flounder for the negative values and by species 16, *Cyclopterus lumpus*, the lump sucker for the positive values.

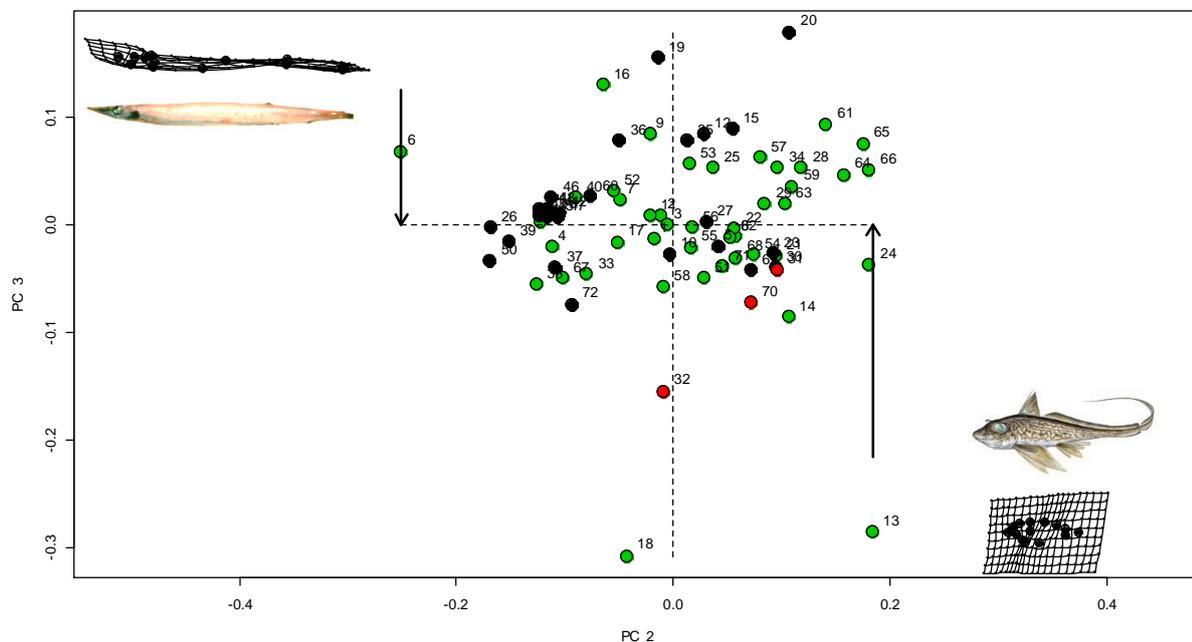


Fig. 7: Tangent space plot of species along the principal axes two and three (PC2 & PC3) with deformation grids of PC2. Fish images represent species with highest positive (on the right) and negative (on the left) PC2 values. Numbers represent species as listed in Table 1. **Black dots:** Arctic species; **green dots:** Boreal species; **red dots:** Arcto-Boreal species; **fish images:** left: *Arctozenus risso*, spotted barracudina (6); right: *Chimaera monstrosa*, rabbit fish (13).

The negative values of shape axis PC2 represent a stretched, elongated body shape with narrow, centered dorsal fins as found in the spotted barracudina (*Arctozenus risso*) in Figure 7. Where the positive values indicate a shorter, roundish to oval shape with the dorsal fins evenly distributed along the dorsal midline, as shown in the deformation grids and represented by the rabbit fish (*Chimaera monstrosa*) in Fig. 7. The spotted barracudina (species 6), represents the extreme on the negative side for PC2, whereas the Rabbit fish (species 13) shows the highest positive PC2 values. In Figure 7, two out of three Arcto-Boreal species, *Triglops pingelii* (70) and *Icelus spatula* (31), lie on the right side of the plot with positive PC2 values, with more oval body shapes and evenly distributed dorsal fins. Boreal species are almost evenly distributed along the PC2 axis and represent both, eel-like and oval body shapes with both narrower and wider dorsal fins. Examples are: the spotted barracudina *Arctozenus risso* (6) with an eel-like body shape and the Norway redfish *Sebastes viviparus* (66) with a more oval body shape. A small cluster of Arctic species lies in the upper left corner with positive PC3 and negative PC2 values, presenting an eel-shaped group in regard to PC2, such as the Arctic eelpout *Lycodes reticulatus* (46) and the longear eelpout *Lycodes seminudus* (48). Arctic species show predominantly positive PC3 values.

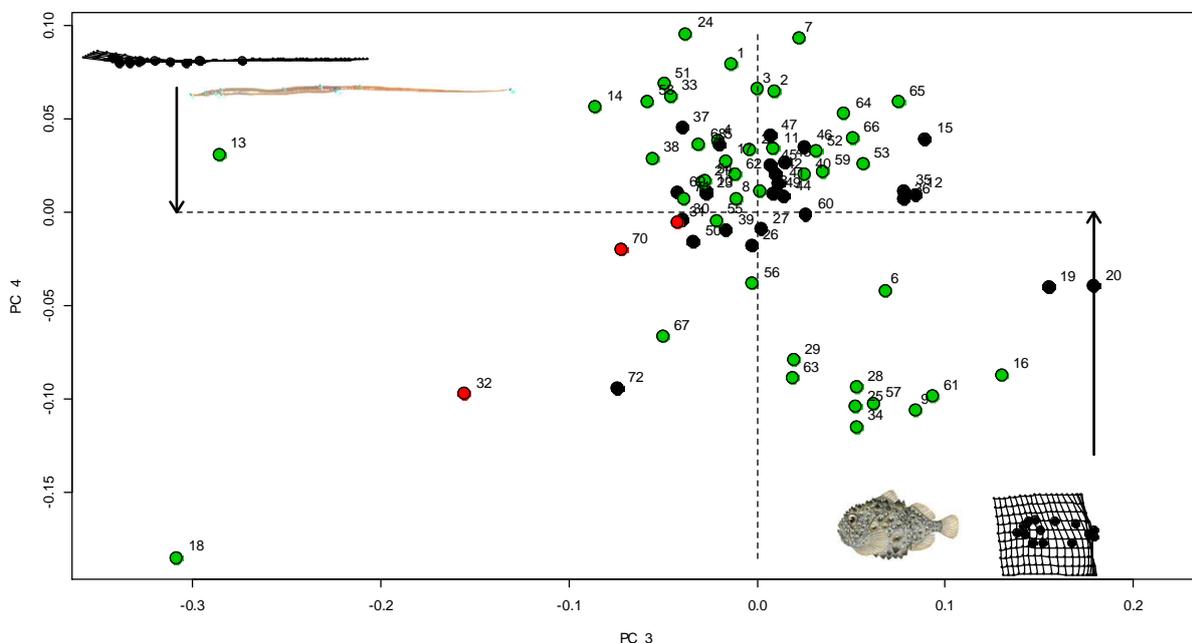


Fig. 8: Tangent space plot of species along the principal axes three and four (PC3 & PC4) with deformation grids of PC3. Fish images represent species with highest positive (on the right) and negative (on the left) PC3 values. Numbers represent species as listed in Table 1. **Black dots:** Arctic species; **green dots:** Boreal species; **red dots:** Arcto-Boreal species; **fish images:** left: *Entelurus aequoreus*, snake pipefish (18); right: *Eumicrotremus spinosus*, Atlantic spiny lumpsucker (20).

The shape axis PC3 picks up on shape differences similar to PC2, where negative values represent a very flat and elongated, eel-like body, with the most extreme shape represented by species 18, *Entelurus aequoreus*, the snake pipefish. Positive PC3 values indicate a shorter, rounder shape with the dorsal and anal fins close towards the caudal fin, where species 20, *Eumicrotremus spinosus*, the Atlantic spiny lumpsucker shows the highest positive values (Fig. 8). In Fig. 8, the Arcto-Boreal species only show negative PC3-values, as they are only present in the lower left part of the plot, presenting slightly elongated body shapes. Boreal species show a small clustering in the lower right corner, representing a group with round body shapes. Round-, oval-shaped species within this cluster are e.g. the lumpsucker *Cyclopterus lumpus* (16), the European plaice *Pleuronectes platessa* (61) and the witch flounder *Glyptocephalus cynoglossus* (25). The remaining Boreal species are distributed evenly around zero of the PC3 axis in the upper half with positive PC4 values, showing both elongated and round body shapes. The arctic fish are clustered around the zero center with the majority on the positive side of PC4 and the positive side of PC3. Therefore, concerning PC3, arctic species show both, elongated bodies as well as round bodies, as represented by the Atlantic herring *Clupea harengus* (14) and the Golden redfish *Sebastes norvegicus* (65). The negative values of shape axis PC4 show deformations such as short heads and short bodies with small mouths and a narrow posterior. Whereas positive values describe wider heads with larger mouths and wider dorsal fins (see deformation grids in Fig. 9). Hence, Boreal and Arctic fish in Fig. 8 showing positive PC4 values present longer and wider heads and slightly longer bodies than fish with negative PC4 values. Species 18, *Entelurus aequoreus*, the snake pipefish, presents the most negative value for PC4 and species 24, *Gasterosteus aculeatus*, the three-spined stickleback, the highest positive one (Fig. 9).

In Fig. 9, two small clusters of Boreal species are present, one in the lower left corner with negative PC4 and PC5 values and one in the lower right corner, with positive PC4 and negative PC5 values. The first cluster on the left hand side resembles a group of fish with small mouths and short heads, where dorsal fins are short based and centered on the dorsal midline (see deformation grid in Fig. 10) with shorter bodies. This cluster consist, with the exception of the glacier lanternfish *Benthoosema glaciale* (9), of flatfish only: witch flounder *Glyptocephalus cynoglossus* (25), long rough dab *Hippoglossoides platessoides* (28), Atlantic halibut *Hippoglossus hippoglossus* (29), common dab *Limanda limanda* (34), lemon sole *Microstomus*

kitt (57), European plaice *Pleuronectes platessa* (61) and Greenland halibut *Reinhardtius hippoglossoides* (63). The cluster on the lower right is composed of the species (53) the silvery lightfish *Maurolicus muelleri*, (52) the capelin *Mallotus villosus*, (14) Atlantic herring *Clupea harengus*, and (7) the greater argentine *Argentina silus*. These species represent an oval body shape and short-based dorsal fins which are evenly distributed along the dorsal midline. The other Arctic and Boreal species are distributed among negative and positive values of PC4 and PC5. The majority of arctic species lies on the right hand side of the plot, with positive PC4 values. Species such as the Arctic cod *Arctogadus glacialis* (5), the Sadko sculpin *Cottunculus sadko* (15) and the Canadian eelpout *Lycodes polaris* (45) represent positive PC4 values in terms of wider heads and evenly distributed, relatively long-based dorsal fins. All three Boreal species lie within the upper left part with positive PC5 and negative PC4 values only, presenting short heads, narrow caudal peduncles and elongated bodies, where dorsal fins are wider and evenly distributed along the dorsal midline (see Fig. 9 and Fig. 10).

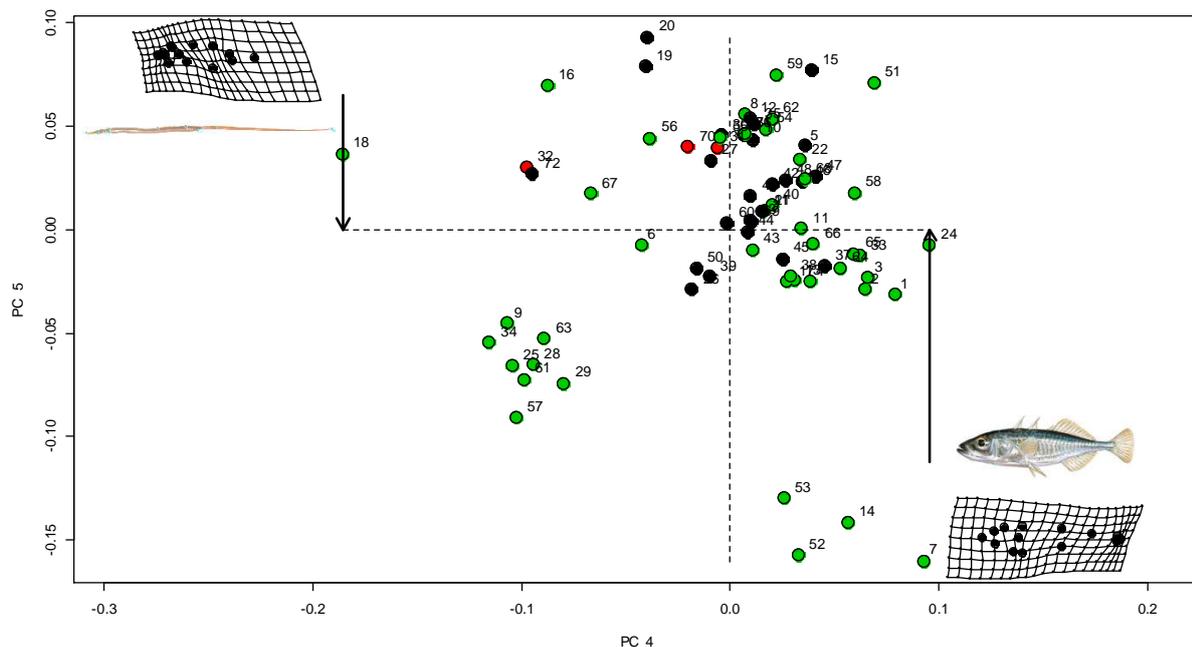


Fig. 9: Tangent space plot of species along the principal axes four and five (PC4 & PC5) with deformation grids of PC4. Fish images represent species with highest positive (on the right) and negative (on the left) PC4 values. Numbers represent species as listed in Table 1. **Black dots:** Arctic species; **green dots:** Boreal species; **red dots:** Arcto-Boreal species; **fish images:** left: *Entelurus aequoreus*, snake pipefish (18); right: *Gasterosteus aculeatus*, three-spined stickleback (24).

In Fig. 10, species are widely distributed along the two shape axis PC5 and PC6. Arctic fish predominantly show positive PC5 values with the majority lying on the right hand side of the plot (Fig. 10). Boreal fish show both negative and positive PC5 values, but the extreme shapes for negative PC5 values are represented by Boreal species only, namely the greater argentine *Argentina silus* (7), the Atlantic herring *Clupea harengus* (14), the capelin *Mallotus villosus* (52) and the silvery lightfish *Maurollicus muelleri* (53). Arcto-Boreal species are found on the positive side of PC5 only. Species 20, *Eumicrotremus spinosus*, the Atlantic spiny lumpsucker, shows the highest value for PC5 on the positive side, where species 7 *Argentina silus*, the greater argentine represents the negative extreme shape (Fig. 10).

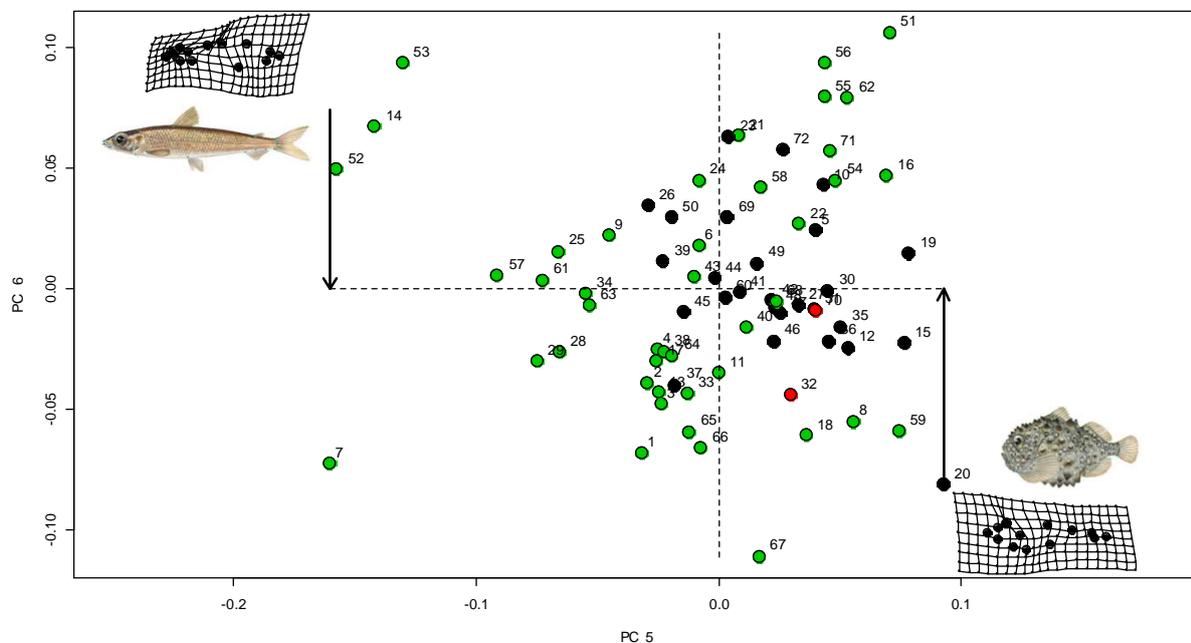


Fig. 10: Tangent space plot of species along the principal axes five and six (PC5 & PC6) with deformation grids of PC5. Fish images represent species with highest positive (on the right) and negative (on the left) PC5 values. Numbers represent species as listed in Table 1. **Black dots:** Arctic species; **green dots:** Boreal species; **red dots:** Arcto-Boreal species; **fish images:** left: *Argentina silus*, greater argentine (7); right: *Eumicrotremus spinosus*, Atlantic spiny lumpsucker (20).

3.2. Analysis of Variance (ANOVA)

3.2.1. Diet

When diet was considered as a factor in the ANOVA, PC2 through PC5 showed no statistically significant results. Only PC1 was significantly associated with diet ($P=0.000144$) (see Fig. 11). Benthos-feeding species showed the lowest mean with a negative PC1 value, indicating small heads and wide anal and dorsal fins for these species. The benthos-group consists of a couple of outliers with positive PC1 values, which describes fish with shorter dorsal and anal fins, located further towards the caudal fin. Benthos/Ichthyophages and Ichthyophages show similar PC1 values and similar means, all with negative PC1 values, representing body shapes with short heads and stretched out dorsal and anal fins from anterior towards the far posterior. Planktonfeeders/Ichthyophages and Planktonfeeders both show a mean within the positive PC1 values where planktonfeeders show the highest positive mean (Fig. 11). The Plankton-feeding groups therefore resemble fish with wider heads and shorter dorsal and anal fins which are located closely towards the caudal fin.

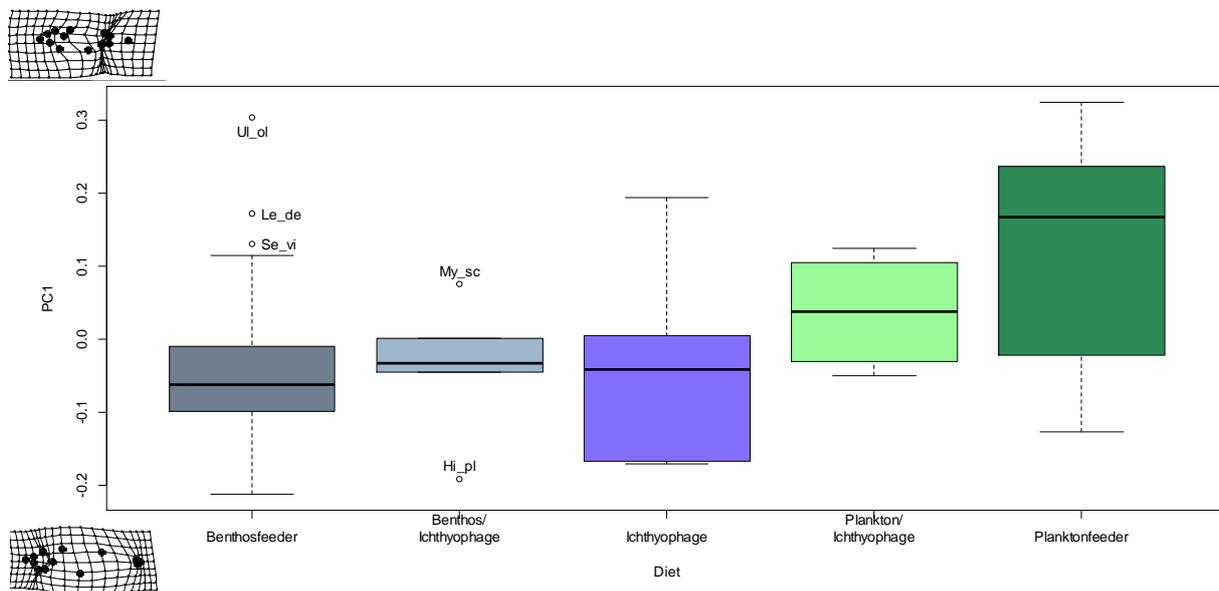


Fig. 11: Box and Whisker plots for the first shape axis (PC1) and the different diet-types with deformation grids of PC1. Mean values are represented by thick black lines within the boxes, and whiskers correspond to minimum and maximum values (where there is no outliers). Outliers marked as dots and labeled with Latin species name abbreviations. **Hi_pl:** *Hippoglossoides platessoides*, American plaice; **Le_de:** *Leptagonus decagonus*, Atlantic poacher; **My_sc:** *Myoxocephalus scorpius*; shorthorn sculpin; **Se_vi:** *Sebastes viviparus*, Norway redfish; **UL_ol:** *Ulcina olrikii*, Arctic alligatorfish.

The interaction of diet and biogeography was also analyzed, though the P-value was only significant for diet and PC1, not for biogeography. From this follows that certain shapes associated with diet are not different between arctic and boreal fish. The box and whisker plot for the interaction of diet and biogeography can be found in the Appendix (App. 2).

3.2.2. Habitat

Habitat was analyzed in relation to the principal components. Only PC1 ($P=0.000654$) and PC5 ($P=0.000654$) were significantly associated with habitat (see Fig. 12). Regarding PC1, the mean for demersal species lies within the negative range of the shape axis (Fig. 12A), therefore species present small heads and outstretched anal and dorsal fins along the lateral and dorsal midline when associated with a demersal habitat. Nevertheless, some species show positive PC1 values within the demersal group (Fig. 12A) and hence present shorter anal and dorsal fins, which are located further towards the caudal fin. Most pelagic species as well as their mean occur within the positive range of PC1, representing shapes with narrow anal and dorsal fins, and wider heads (Fig. 12A).

As for PC5, demersal fish show a slightly higher mean than pelagic fish for PC5, though both lie around zero (Fig. 12B). Pelagic species show a wider range within the negative values of PC5, which makes this group rounder in shape, with wider dorsal fins, centered along the dorsal midline. The PC5-range for demersal fish covers both negative and positive values (Fig. 12B). Hence, both shape deformations of PC5, short heads and centered narrow dorsal fins, as well as wider heads and wider dorsal fins, can be found within pelagic fish.

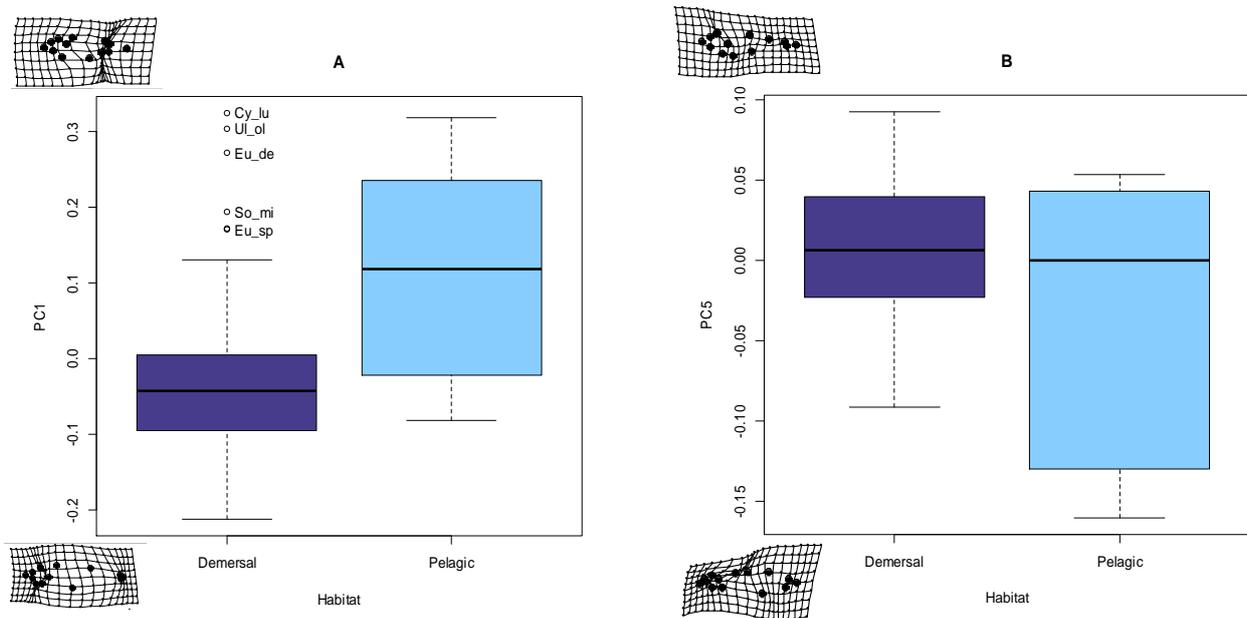


Fig. 12: Box and Whisker plots for the shape axis PC1 and PC5, and the different habitat-types with deformation grids of PC1 and PC5. Mean values are represented by thick black lines within the boxes, and whiskers correspond to minimum and maximum values (where there is no outliers). Outliers marked as dots and labeled with Latin species name abbreviations. **A.** Shape axis one (PC1) in relation to habitat. **B.** Shape axis five (PC5) in relation to habitat. **Cy_lu:** *Cyclopterus lumpus*, lump sucker; **Eu_de:** *Eumicrotremus derjugini*, Leatherfin lump sucker; **Eu_sp:** *Eumicrotremus spinosus*, Atlantic spiny lump sucker; **So_mi:** *Somniosus microcephalus*, Greenland shark; **Ul_ol:** *Ulcina olrikii*, Arctic alligatorfish.

3.2.3. Biogeography

Biogeography was analyzed as a factor in the ANOVA. PC2 ($P=0.00803$), PC3 ($P=0.0493$), and PC5 ($P=0.00422$) showed significant differences with regard to the biogeographic categories Arctic, Arcto-Boreal, and Boreal.

Concerning shape axis PC2, Arctic species show a negative mean and predominantly lie within the negative range of PC2 (Fig. 13A). This makes the arctic species a group of elongated, eel-like fish. Both, Arcto-Boreal and Boreal fish present a positive mean regarding PC2 (Fig. 13A), presenting more oval shapes. However, few Boreal species present shapes with elongated bodies within the negative range of PC2.

In Fig. 13B, Arctic species show a mean slightly above zero whereas the mean for Boreal species lies just below zero for PC3. Hence, both Arctic and Boreal fish present positive as well as negative values for shape axis PC3. This indicates that eel-like and oval body shapes can be

observed in both groups. Arcto-Boreal fish, however, exhibit negative PC3 values only, which clearly classes them into the group of eel-like body shapes.

For shape axis PC5, Arctic and Arcto-Boreal fish show a positive mean (Fig. 13C). Arcto-Boreal species present positive PC5 values only, and Arctic fish are found predominantly within the positive range. Hence, both groups have wider heads and wider dorsal fins, evenly distributed along the dorsal midline. Boreal fish present a negative mean in regards to PC5 where species show positive and negative values (Fig. 13C). This indicates a distribution of small mouths and narrow dorsal fins as well as wider mouths and wider dorsal fins within the boreal group.

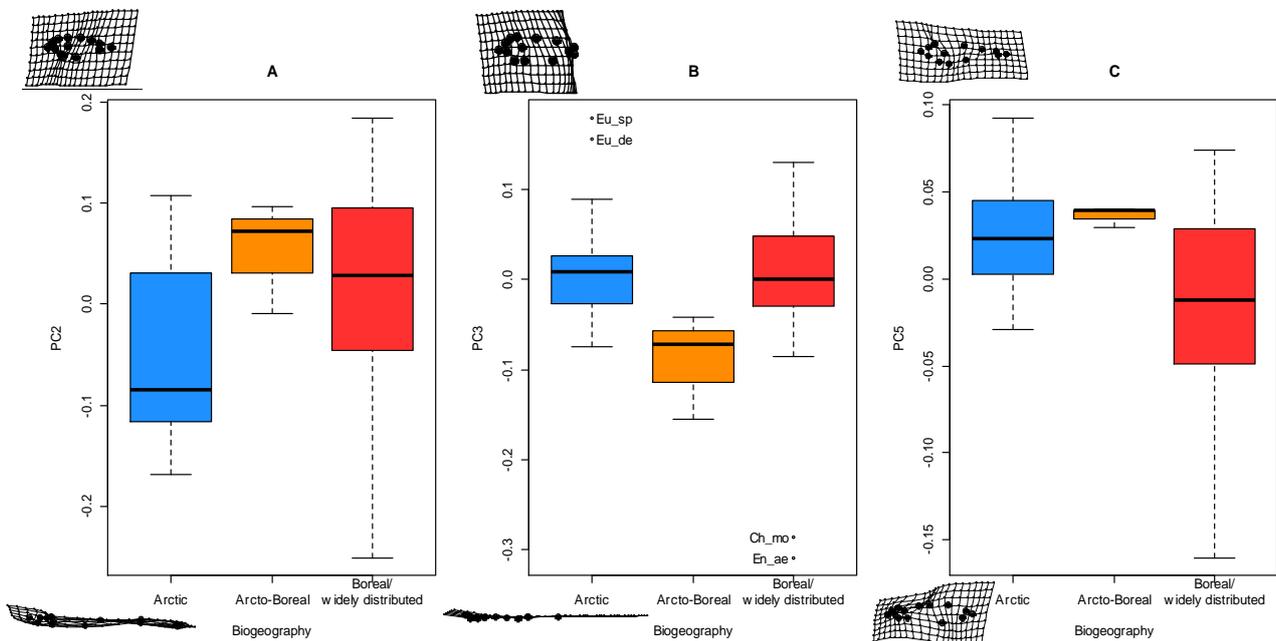


Fig. 13: Box and Whisker plots for the shape axis PC2, PC3 and PC5 of Arctic, Arcto-Boreal and Boreal species and the different biogeography-types with deformation grids of PC2, PC3, and PC5. Mean values are represented by thick black lines within the boxes, and whiskers correspond to minimum and maximum values (where there is no outliers). Outliers marked as dots and labeled with Latin species name abbreviations. **A:** Shape axis two (PC2) in relation to Biogeography. **B:** Shape axis three (PC3) in relation to Biogeography. **C:** Shape axis five (PC5) in relation to Biogeography. **Ch_mo:** *Chimaera monstrosa*, Rabbit fish; **En_ae:** *Entelurus aequoreus*, snake pipefish; **Eu_de:** *Eumicrotremus derjugini*, leatherfin lump sucker; **Eu_sp:** *Eumicrotremus spinosus*, Atlantic spiny lump sucker.

3.2.4. Biogeography and Habitat

Biogeography was analyzed with habitat as an additional factor. The shape axis PC1 ($P=0.00094$) and PC5 (0.0301) were significant for habitat only. Hence, habitats and their corresponding shape association do not differ between Arctic and Boreal fish. Yet habitats are significantly different in relation to shape in Barents Sea fish. Both demersal Arctic and demersal

Boreal species show a similar range in PC1 values and a negative mean (Fig. 14A). So they present body shapes with small heads and long-based dorsal and anal fins stretching from the anterior to the posterior. In the contrary, pelagic species, both Arctic and Boreal, show much higher PC1 values and a positive mean (Fig. 14A). Such pelagic fish show wider heads and narrower dorsal fins, located closely towards the caudal fin. Concerning PC5, both demersal and pelagic species show similar means slightly above and below zero, regardless of their biogeographic affiliation (Fig. 14B). Nevertheless, pelagic fish present a much wider range within the negative PC5-values than demersal species (Fig. 14B). This indicates that pelagic species are associated with wider heads and wider dorsal fins, distributed evenly along the dorsal midline.

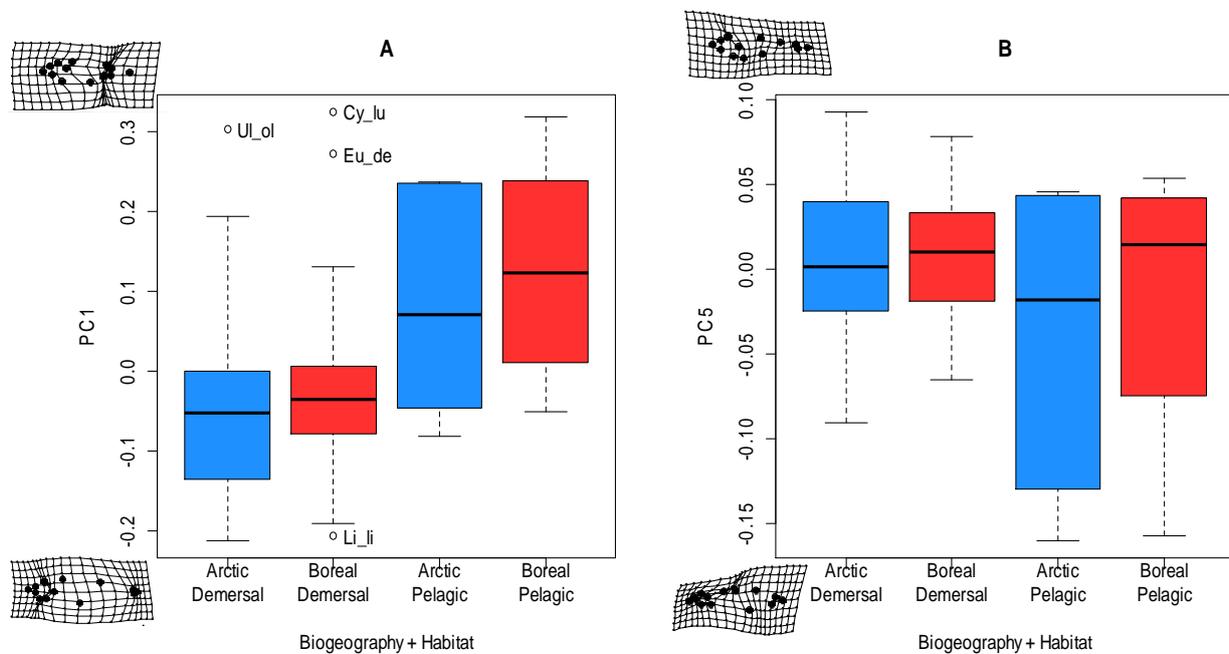


Fig. 14: Box and Whisker plot for the shape axes PC1 and PC5, and the different habitat-types with deformation grids of PC1 and PC5. Mean values are represented by thick black lines within the boxes, and whiskers correspond to minimum and maximum values (where there is no outliers). Outliers marked as dots and labeled with Latin species name abbreviations. **A:** Shape axis one (PC1) in relation to Biogeography and Habitat. **B:** Shape axis five (PC5) in relation to Biogeography and Habitat. **Cy_lu:** *Cyclopterus lumpus*, lumpsucker; **Eu_de:** *Eumicrotremus derjugini*, leatherfin lumpsucker; **Li_li:** *Limanda limanda*, common dab; **Ul_ol:** *Ulcina olrikii*, Arctic alligatorfish.

3.3. Redundancy Analysis (RDA)

3.3.1. Biogeography and Diet

The RDA of biogeography and diet has a total inertia equal to 0.03994 and the part of this inertia explained by the biogeography-diet variable is equal to 0.00888, or 22.23% of the total. A permutation test shows that the relationship between shape (PCs) and biogeography-diet is significant ($P=0.005$). The RDA biplot is shown in Fig. 15.

In Fig. 15, the centroid for Arctic species is found in the lower left part of plot and stands in opposition to Arcto-Boreal and Boreal centroids, lying in the upper right part. Regarding the diet centroids, Benthosfeeders and Benthos/Ichthyophages (on the left) pose an opposition to Planktonfeeders, pointing in the opposite direction towards the right (Fig. 15). The centroid for Ichthyophages lies closer to Benthosfeeders and Benthos/Ichthyophages, whereas Plankton/Ichthyophages are more associated with Planktonfeeders, both lying on the left side. Arctic species (blue in plot) form a cluster on the lower left, indicating their association with positive values of the shape axes PC4 and PC5. Positive values of these two shape axes describe fish with wider heads and wider dorsal fins. This cluster of Arctic fish also corresponds with Benthosfeeders and Benthos/Ichthyophages on the left. For example, some species of the Genus *Lycodes* (e.g. *Lycodes eudipleurostictus* (Ly_eu), *Lycodes squamiventer* (Ly_sq)) as well as *Lycodonus flagellicauda* (Ly_fl) show a clear pattern towards a Benthosfeeding-diet in the plot. However, some Arctic fish are also present in the lower right and upper part of the plot, closer to Ichthyophages or Planktonfeeders, with positive PC1 and PC2 values. This can be seen on Arctic species such as the alligator fish, *Ulcina olrikii* (Ul_ol) and species of the genus *Eumicrotremus* (leatherfin lumpsucker (Eu_de) and Atlantic spiny lumpsucker (Eu_sp)) lying towards the far right, close to Plankton-diet and positive PC1. In regards to shape, this indicates the presence of narrower dorsal and anal fins which are located further towards the caudal fin in these fish.

Two of the three Arcto-Boreal fish, the spatulate sculpin, *Icelus spatula* (Ic_sp) and the ribbed sculpin *Triglops pingelii* (Tr_pi), lie within the upper part of the plot (Fig. 15). Both species show negative values for all shape axes except for PC2. This indicates a more oval body shape with dorsal fins evenly distributed along the dorsal midline. The third Arcto-Boreal fish, *Leptagonus decagonus* (Atlantic poacher (Le_de)) is associated with a positive PC1 value, a shape with narrow anal and dorsal fins, moved further towards the posterior.

Boreal species are found within all four quadrants of the plot, showing a wider diversity in diet and shape among the fish (Fig. 15). Clusters of Boreal fish are present in the upper left as well in the lower left, with species such as the slender eelblenny, *Lumpenus lamprettaeformis* (Lu_la) and the witch flounder, *Glyptocephalus cynoglossus* (Gl_cy) showing a close relation to Benthos, Benthos/Ichthyophage and Ichthyophage diet-types (Fig. 15). The cluster on the lower left shows positive PC4 and PC5 values and therefore shapes with wider heads and wider dorsal fins are present in this group. The cluster on the upper left, in the contrary, shows negative PC4 and PC5 values, presenting short heads and elongated body shapes. The Boreal species located on the right side of the plot, show their affiliation towards a plankton-diet and shapes according to positive PC1 and PC2 values. These shape axes describe slightly elongated body shapes where dorsal fins are narrow and located further towards the posterior. In general, the biplot in Figure 13 illustrates how the positive values of shape axes PC1 and PC2 are associated with a Plankton and Plankton/Ichthyophage kind of diet. In the contrary, PC3, PC4, and PC5 are more important for Benthos-feeders and Ichthyophages (Fig. 15).

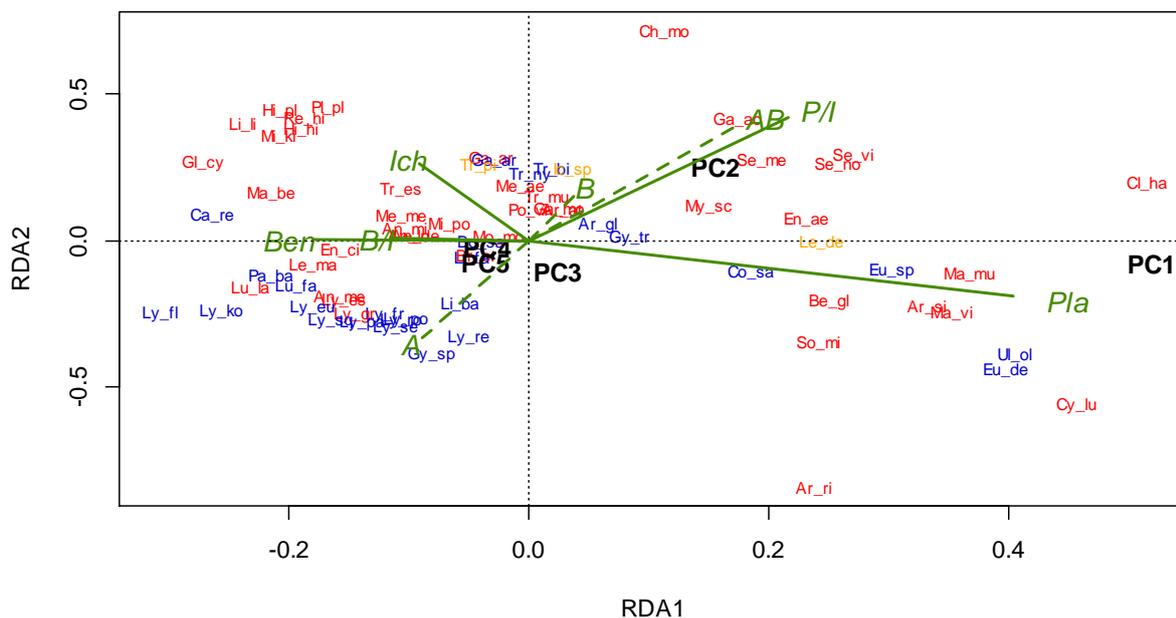


Fig. 15: Biplot of RDA discriminant analysis of the biogeography-diet groups with the centroids of the factors shown in the plot. First five principal components (PC) are plotted. Fish are labelled with their latin species name abbreviations and color coded according to their biogeographical affiliation. Coordinates of the biogeography and diet variables have been multiplied by 2.5 and the coordinates of the PC variables by 7 to make them more legible. **Red:** Boreal; **Orange:** Arcto-Boreal; **Blue:** Arctic; **A:** Centroid for Arctic; **AB:** Centroid for Arcto-Boreal; **B:** Centroid for Boreal; **Ben:** Benthosfeeder; **B/I:** Benthos/Ichthyophage; **Ick:** Ichthyophage; **P/I:** Plankton/Ichthyophage; **Pla:** Planktonfeeder; **PC1-PC5:** Principal component centroids one to five.

3.3.2. Biogeography and Habitat

The RDA of biogeography and habitat has a total inertia equal to 0.03994, where the biogeography-habitat variable's inertia is equal to 0.00549, explaining 13.75% of the total inertia. A permutation test shows that the relationship between shape (PCs) and biogeography-habitat is significant ($P=0.005$).

The RDA biplot with Biogeography and Habitat in Fig. 16 shows similar species clustering and PC-centroid distribution as the biplot in Fig. 15. The biogeographic centroids Boreal and Arcto-Boreal stand in opposition with the Arctic, and the demersal opposes the pelagic centroid (Fig. 16).

The shape axis PC1 and PC2 point towards the right, whereabouts Arctic, Arcto-Boreal, and Boreal species are associated with their positive values. The habitat centroid 'pelagic' is also located on the left side of the plot, highlighting its affiliation with the two shape axes PC1 and PC2 (Fig. 16). Species associated with a pelagic habitat and narrow dorsal fins, according to positive PC1, are: the snake pipefish, *Entelurus aequoreus* (En_ae), the Atlantic herring, *Clupea harengus* (Cl_ha), and the silvery lightfish, *Maurolicus muelleri* (Ma_mu) (see Fig. 16). Fish such as the three-spined stickleback, *Gasterosteus aculeatus* (Ga_ac) and the Arctic cod, *Arctogadus glacialis* (Ar_gl) represent species with a pelagic habitat and positive PC2 values, indicating oval body shapes.

Arctic species cluster predominantly on the lower left side of the plot, presenting a demersal habitat type and positive values for the shape axes PC3 and PC5 (Fig. 16). Hence, species like the black seasnail, *Paraliparis bathybius* (Pa_ba), the gelatinous snailfish, *Liparis fabricii* (Li_fa), and the doubleline eelpout, *Lycodes eudipleurostictus* (Ly_eu) resemble body shapes where the anterior dorsal fin insertion is close to the operculum and live in demersal habitats.

Boreal fish are predominantly found in the upper left corner, with a demersal habitat and positive PC2 and PC3 affiliation. Concerning shape, these species show wider heads, as represented in the plot by species such as the roughhead grenadier, *Macrourus berglax* (Ma_be), the common dab, *Limanda limanda* (Li_li) and the witch flounder, *Glyptocephalus cynoglossus* (Gl_cy) (Fig. 16).

In general, the biplot in Figure 16 illustrates how positive PC1 and partly PC2 values are more important for pelagic species. For demersal fish, the shape axes PC3, PC4 and PC5 are more relevant.

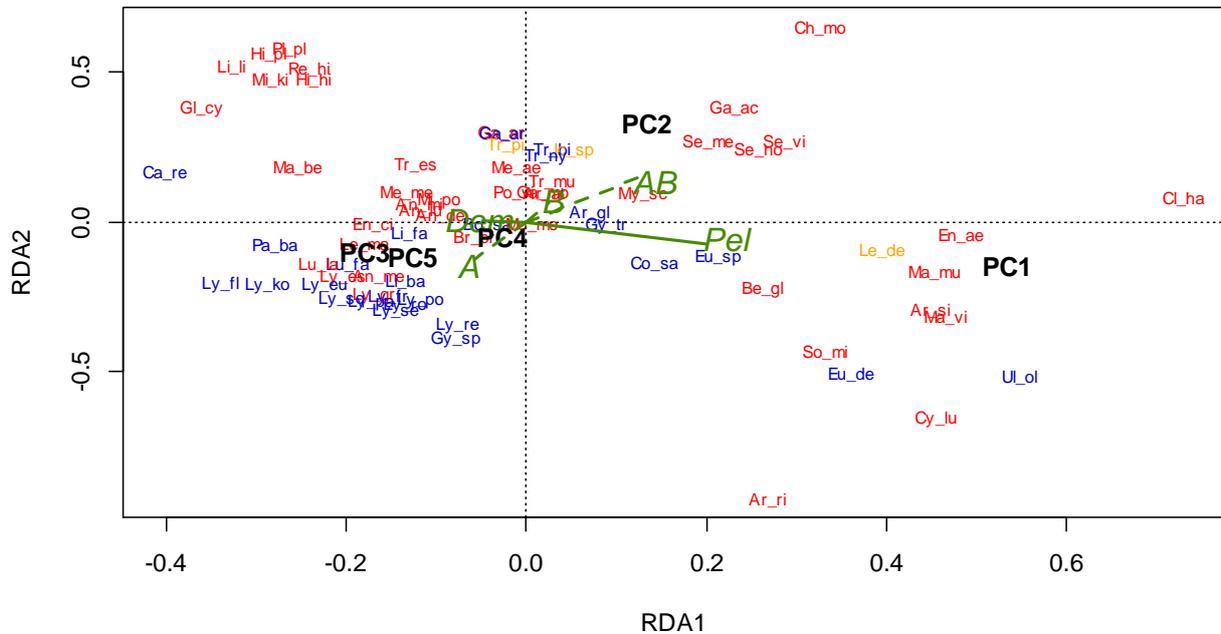


Fig. 16: Biplot of RDA discriminant analysis of the biogeography-habitat groups with the centroids of the factors shown in the plot. First five principal components (PC) are plotted. Fish are labelled with their latin species name abbreviations and color coded according to their biogeographical affiliation. Coordinates of the PC variables have been multiplied by 10 to make them more legible. **Red:** Boreal; **Orange:** Arcto-Boreal; **Blue:** Arctic; **A:** Centroid for Arctic; **AB:** Centroid for Arcto-Boreal; **B:** Centroid for Boreal; **Dem:** Centroid for Demersal habitat; **Pel:** Centroid for pelagic habitat; **PC1-PC5:** Principal component centroids one to five.

3.4. Mapping

The Procrustes transformed species shapes were mapped at their mass center of distribution to highlight shape variation in space. The map in Fig. 17 shows how species further to the North have slightly more elongated, eel-like body shapes, such as the Atlantic hookear sculpin *Artediellus atlanticus* (Ar_at), the ribbed sculpin *Triglops pingelii* (Tr_pi), *Careproctus* sp. (Ca_re) and the Atlantic poacher *Leptagonus decagonus* (Le_de). Species with their distribution centroids located further within the central and south-western Barents Sea, show slightly rounder, more oval body outlines, e.g. European plaice *Pleuronectes platessa* (Pl_pl), Long rough dab *Hippoglossoides platessoides* (Hi_pl), Lemon sole *Microstomus kitt* (Mi_ki). The shape of the leatherfin lumpsucker *Eumicrotremus derjugini* (Eu_de) sticks out in the North, with a more oval shape in comparison to the surrounding species with more elongated bodies. In the southeast, the fourbearded rockling *Enchelyopus cimbrius* (En_ci), the roughhead grenadier *Macrourus berglax* (Ma_be) and the blue whiting *Micromesistius poutassou* (Mi_po) show relatively narrow, elongated bodies. A larger version of the map can be found in the appendix (App. 3).

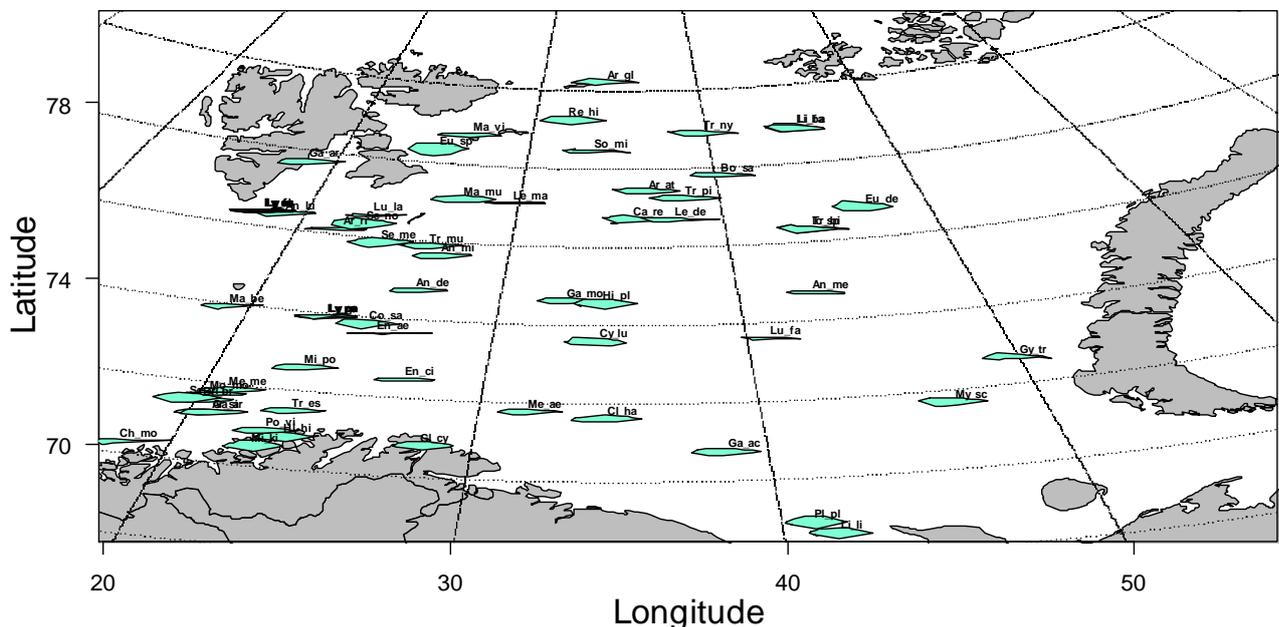


Fig. 17: Map of the Barents Sea with Procrustes transformed species shapes plotted at their mass center of distribution. Labels according to Latin species name abbreviations as listed in Table 1.

4. Discussion

4.1. Shape variation

The main shape variation within the Barents Sea fish community is found within two morphological characteristics:

- (1) in body shape: from eel-like to oval and roundish bodies
- (2) in anal and dorsal fins: either equally distributed along the dorsal midline and/or long-based or located close towards the posterior and/or short-based.

In the literature, variation in body shape and fins is often correlated with the swimming mode. This is because locomotory performance stands under strong selective pressure as all fish swim in order to escape, feed or mate, and is therefore thought to play a key role in the diversification of fish (Tytell et al., 2010). In general, a continuum of different swimming modes and their association with certain body shapes have been recognized and applied to a large number of different fish (Helfman, Collette, & Facey, 1997). This continuum goes from (1) the anguilliform mode to (2) the carangiform mode. Anguilliform swimming occurs in slender-bodied, eel-like and elongated fish, presenting undulatory locomotion (Liao, 2002). The elongated *Lycodes* species have been reported to use anguilliform locomotion (Stein, Felley, & Vecchione, 2005). The ten fish of the genus *Lycodes* assessed in this study can therefore be assumed to be anguilliform swimmers. Fish from the genera *Liparis* and *Lumpenus* cluster with *Lycodes* species in Fig. 6 and show the same morphological characteristics as *Lycodes*, with elongated body shapes and long-based anal and dorsal fins stretching along the dorsal and lateral midline. These fish most likely exhibit the same swimming mode.

Carangiform swimmers show much less motion in their bodies and their body shapes are 'mackerel-like', and more streamlined (Lauder & Tytell, 2006). The saithe *Pollachius virens* is an example of the carangiform mode (Cheng & Blickhan, 1994). In terms of shape, saithe clusters with Atlantic cod *Gadus morhua*, Arctic cod *Arctogadus glacialis*, blue whiting *Micromesistius poutassou*, haddock *Melanogrammus aeglefinus* and polar cod *Boreogadus saida* (Fig. 6). They all show similar streamlined bodies, as well as similar anal and dorsal fin base-lengths and fin distributions along the dorsal and lateral midline. These species can therefore be assumed to belong to the carangiform swimmers.

In other, more detailed categorizations of fish locomotion not only shape but also fins have been described to influence swimming performance. In a publication by Webb (1984), different

swimming modes are summarized, such as: (1) Body/Caudal Fin (BCF) periodic propulsion where locomotor movements repeat; and (2) Body/Caudal Fin (BCF) transient propulsion with brief and non-cyclic movements.

In Body/Caudal Fin (BCF) periodic propulsion fish show a narrow caudal peduncle and a stiff, streamlined body with large anterior depth. The optimal morphology for BCF periodic swimmers is the thunniform design as found in Tunas (Thunnidae), with streamlined bodies and very short-based dorsal and anal fins. However, there is still morphological variation in fish exhibiting such swimming mode. In general, BCF periodic propulsion is optimized and usually exhibited by fish with small body/fin areas (see Webb, 1984 and references therein). Such swimming mode with steady velocities and cruising has been proposed for sticklebacks swimming in the open water (J. A. Walker, 1997). The pelagic three-spined stickleback is likely to show such BCF periodic propulsion. Interestingly, the stickleback clusters with the redfish *Sebastes mentella*, *Sebastes norvegicus* and *Sebastes viviparus* and also with the rabbit fish *Chimaera monstrosa* (Fig. 6). And indeed, steady swimming has already been reported for redfish (Beamish, 1978). Therefore, these species exhibit most likely the same or at least very similar swimming modes. This might also apply for the rabbit fish.

In BCF transient propulsion fish present a large body depth along the body length, especially caudally. One extreme example is presented by the cottid fish form (from Cottidae) where morphology maximizes transient swimming ability, such as in the Atlantic hookear sculpin *Artediellus atlanticus*. These fish show an extension of the body's dorso-ventral depth along the whole length through long-based dorsal and anal fins. The BCF transient performance is morphologically optimized by a large body/fin area (see Webb, 1984 and references therein).

Fast starts exhibited by fish are also considered a transient (unsteady) motion. Fast start swimming has been reported for the herring (*Clupea harengus*) and the shorthorn sculpin (*Myoxocephalus Scorpius*) by Domenici and Blake (1997). The herring and all the sculpin species assessed in this present study, including the hookear sculpin, show similar PC2 values, lying adjacent to each other in Fig. 6, presenting streamlined body shapes. It is very likely that the different sculpin species will show a similar swimming mode to that of the hookear and shorthorn sculpin.

The swimming modes described above are mostly associated with locomotor specialist, species which have specialized in one of these forms of swimming. Unspecialized fish are referred to as generalist swimmers, which are generally far more numerous. Such generalists usually overlap

locomotor modes and shapes of specialists (Webb, 1984). The Atlantic cod belongs to the generalist swimmers (Reidy, Kerr, & Nelson, 2000) and clusters with the other cod species, as well as saithe and blue whiting (Fig. 6). In the biplot (Fig. 6) they are located in the center, between the locomotor specialists such as sticklebacks, herring and the eel-like fish (e.g. *Lycodes*). This locomotor overlap confirms the morphological overlap as these fish are lying centered between the 'extreme shapes'. It has been shown that fish using the same propulsion method also display similar morphology (Sfakiotakis, Lane, & Davies, 1999).

However, each swimming mode will define a fish's performance boundaries by using a certain structure. These boundaries in return will then most likely constrain a species' options of behaviors (Webb, 1984). Shape variations and the resulting swimming mode are most likely adaptations to certain ecology, such as feeding behavior and diet and the associated habitat (Helfman et al., 1997). Therefore, some authors discuss different fish swimming modes and their implications by relating species shapes and locomotor variation to ecological differences (e.g. Assumpção et al., 2012; Farré, Tuset, Maynou, Recasens, & Lombarte, 2013; Schleuter et al., 2012).

4.2. Ecological implications of shape variation

Morphology and swimming performance have been shown to be related to resource use (Sampaio, Pagotto, & Goulart, 2013). Hence, body shape and locomotory patterns are likely to be morphological adaptations for feeding behavior (Helfman et al., 1997).

Webb (1984) related swimming modes and shape to the distribution characteristics of food. Food distribution and dispersal influence the role of locomotion in search and capture. Food varies in distribution in time and space as well as in evasive capabilities. So in order to use it as a resource, different swimming performances are required. He further argues that certain swimming modes serve to capture different kinds of prey. BCF periodic swimming fish with streamlined bodies and large anterior depth are associated with food largely dispersed in time and space (Webb, 1984). This, however, can still indicate a large variety of different food sources. The group identified as BCF periodic swimmers, containing the three-spined stickleback and three different red fish does not indicate a common diet. Those species are associated with very different diets, such as planktivorous, piscivorous and benthivorous feeding.

On the other hand, BCF transient swimmers with large body length are likely to prey on evasive items which are usually locally abundant (Webb, 1984). The sculpins assessed in this study

exhibiting BCF transient propulsion show very similar diets, with all of them being benthosfeeders. The same applies for the rabbit fish, also belonging to this swimming mode group. In contrast, the Arctic cod (*Arctogadus glacialis*) and the silvery pout (*Gadiculus argenteus*) show a planktonic diet, whereas the Arctic rockling (*Gaidropsarus argentatus*) is associated with a benthic and piscivorous diet. This indicates how fish with similar shapes and swimming modes can feed on diet with the same characteristics (locally abundant and evasive) but the diet itself still varies drastically.

Sampaio et al. (2013) revealed how different morphological patterns in Cichlid fish imply different forms of resource exploitation. In their study, one cichlid fish species feeding on detritus showed a higher width of the caudal peduncle and higher areas of the pectoral and pelvic fin. Whereas another species feeding mostly on fish and crustaceans showed higher values for the area of the anal fin and the width of the peduncle. Unfortunately, the caudal peduncle could not be taken into account in this study (after landmarks were removed), as Barents Sea fish were too diverse and sometimes showed no curvature on the caudal peduncle or did not present one at all.

Yet, the findings by Sampaio et al. (2013) regarding the importance of differences in fin areas only partly confirm the findings in this study. The authors find the main shape differences within anal, pelvic and pectoral fin to be related to different diets. In Barents Sea fish, differences in diet seem to be strongly related to differences in the location of dorsal and anal fins and their base-length. Nevertheless, larger fin areas usually also imply a wider fin base and in this present study anal and dorsal fins appear to be the main drivers for diet differences (PC1 for diet in Fig. 11).

Attention has to be paid indeed, when drawing conclusions from shape variations in fish. A review on piscivorous fish by Juanes, Buckel, and Scharf (2002) highlighted how fish with the same or similar diet can be morphologically very different. For example, tuna species (Scombridae) with large, streamlined bodies and large anterior body depth differ dramatically from trumpetfish (Aulostomidae) with long slender bodies and a long snout. Both are considered piscivorous, though, and in this case shape differences are related to varying behavioral patterns, not to diet (Juanes et al., 2002). Such observations are also found in the Barents Sea, where elongated, eel-like fish e.g. the stout eelblenny *Anisarchus medius* and round flatfish e.g. the common dab *Limanda limanda* are both considered benthivores but are very different in shape. However, differences in overall body shape do not seem as important in relation to diet

differences. It is more the fin location and base length that distinguishes between diet types for different shaped fish. Both fish named above, the stout eelblenny and the common dab, show different body shapes but the same long-based anal and dorsal fins. Therefore this study highlights how fins can explain diet differences/similarities that body shape cannot.

However, in most ecomorphological studies on fish, not only diet, but other factors such as habitat are taken into account for analysis. This is because body shape and swimming ability are often related to habitat use. The structure of a habitat forces fish to possess certain swimming abilities to successfully perform maneuvers in order to e.g. hide, capture prey and escape, which will then be reflected in the morphology of a fish accordingly. Gatz (1979) demonstrated how fish with dorsal mouths feed more in the upper water column, whereas fish with ventral mouths feed close to the bottom within the lower water column. Sampaio et al. (2013) identified significant ecomorphological differences for different habitat types in cichlid fish. In Barents Sea fish, the most significant shape variation in relation to habitat differences is again found within the location and base-length of the paired fins. The resolution of the mouth landmarks, unfortunately, was not high enough in this present study.

Concerning the fins, morphological differences in the relative area of the pelvic fin can give information on what kind of habitat a fish uses. Larger pelvic fins indicate benthic species, where smaller fins indicate pelagic fish (see Sampaio et al., 2013 and references therein). For benthic species, the importance of well-developed pelvic and pectoral fins has been reported in order for the fish to stabilize the body on the substrate. The rabbit fish *Chimaera monstrosa*, and the three redfish assessed in this study, for example, represent demersal species with relatively large pelvic fins but the size of the pelvic fins was not considered in this study. Demersal fish are also strongly associated with eel-like, elongated body shapes, as well as round-shaped flatfish (Helfman et al., 1997). Elongated fish exhibiting an anguilliform swimming mode are also strongly associated with a benthic environment (Helfman et al., 1997). This seems to be applicable for the eel-like Barents Sea fish, as many of them are associated with a demersal habitat (Table 1). But statistically, no significant difference was found between demersal and pelagic species considering the overall body shape. Yet, once again the location of the anal and dorsal fins and their base length distinguished fish from different habitats. Unfortunately, no similar findings have been reported in the literature so far. But interestingly, body shapes of fish presenting long-based anal and dorsal fins correspond with how Helfman et al. (1997) described body shapes for demersal fish, namely eel-like and elongated as well as flatfish shaped.

Pelagic species on the contrary, present more compressed bodies with fusiform body shapes (Oliveira et al., 2010). Examples found in this study are species such as the herring, Arctic cod, polar cod and the silvery pout. In general, Johnston and Camm (1987) found carangiform swimmers with fast starts to be usually pelagic. This only partly confirms the findings in this study, where fish assumed to exhibit the carangiform swimming mode are demersal. Though some uncertainty lies in the swimming mode assumption and many species might be more generalist rather than specialist swimmers. Therefore similar shapes might still indicate different habitat choices. But again, the shape differences found in this study for the different habitats are more strongly related to the fin location and base-length (Fig. 12) and not significant for round or elongated body shapes.

Regarding biogeography, no implications for fish morphology have been documented. In the available literature no correlations between shape and biogeographic association are found. This partly confirms the findings in this study, as no significant differences in anal and dorsal fin location (PC1) were found (Fig. 13). A still noteworthy observation, though, is that arctic species present slightly more eel-like body shapes than boreal fish (Fig. 13A) which could be hypothesized as an adaptation to life under the ice.

Nevertheless, diet and habitat seem to be more important drivers for shape variation than biogeography and temperature.

4.3. Relating shape to function

In many ways, morphology is often related to certain functions.

Wiedmann (2014) identified several functional fish groups within the Barents Sea, partly based on morphology. One group, with ‘large demersal’ fish in his study included some flatfish and other species with very long-based anal and dorsal fins, such as the roughhead grenadier. Interestingly, almost all named species within Wiedmann’s group are in accordance with the boreal-demersal cluster of flatfish and others as identified in the PCA (upper left in Fig. 6). These species resemble predators at high trophic levels which require plenty of energy. But at the same time, these fish can also hold large amounts of energy and are therefore able to distribute it over large temporal and spatial scales (Wiedmann, 2014). In the Aegean Sea, flatfish were found to serve as a link between lower and higher trophic levels. Therefore they are essential for the flow of energy produced by the benthos to other parts of the ecosystem (Karachle & Stergiou, 2011).

Another group of fish identified by Wiedmann (2014) consisted of 'long-demersals'. All species in this category presented either elongated or eel-like body shapes. These types of fish are stationary as they are not very good long-distance swimmers. Therefore, they are very efficient in using local benthic resources (Wiedmann, 2014).

Functions also comprise different swimming behaviors in order to fulfill certain tasks, for example searching for particular prey or finding mating partners. For instance, Webb (1984) classes different locomotor propulsion mechanisms to various functions. Fish with large body depths exhibiting Body Caudal Fin (BCF) transient propulsion use this swimming mode for fast starts and powered turns for prey capture and predator invasion. This is characteristic for fish of the family Cottidae, such as the Atlantic hookear sculpin *Artediellus atlanticus* which feeds on polychaetes, gammarids and other invertebrates (Wienerroither, 2011). The morphology and swimming mode described serve as a way to obtain maximum acceleration in order to catch prey before it can maneuver or reach shelter (Webb, 1984). This might also apply to the other sculpin species in this study, as they most likely perform a similar swimming mode and show similar diets with most of them feeding on benthos.

Body caudal fin periodic propulsion is used in fish that need to sustain swimming for several seconds to several weeks in cruising, prolonged and sprint swimming and migration.

These usually pelagic fish are for example the capelin (*Mallotus villosus*) and the herring (*Clupea harengus*) which show very streamlined bodies and both conduct large migrations through the Barents Sea (Wienerroither, 2011). Such migrating species often play key roles in ecosystems, as do herring and capelin in the Barents Sea (Wassmann et al., 2006). Capelin is a very specialized plankton feeder and the most important planktivore in the Barents Sea (Gjørseter, 1998; Hamre, 1994). Capelin feeds heavily on mesozooplankton and represents a strong link between higher and lower trophic levels. These fish conduct a massive northward feeding migration which is thought to be an adaptation to exploit the plankton production as the ice edge recedes (Sakshaug & Skjoldal, 1989). The importance of capelin as prey was highlighted by Dolgov (2002), who found that 20 different fish species alone feed on capelin and that it seems to be the most important food source for Atlantic cod. Additionally, capelin is also found in the diet of various seabirds, seals and cetaceans. And not only the adult fish, but also its eggs are consumed by haddock, and its larvae are eaten by herring (Dolgov, 2002; Huse & Toresen, 2000). Hence, such migratory behavior as found in the capelin transports energy in the form of resources throughout the system (Dolgov, 2002; Varpe, Fiksen, & Slotte, 2005). Such

findings have also been reported for herring in the Norwegian Sea, but this migratory species also impacts the Barents Sea (Varpe et al., 2005). Herring spawning products provide an enormous food source for animals along the coast and immature herring are an important prey in the Barents Sea (Varpe et al., 2005; Wienerroither, 2011).

Overall, shapes and functions associated with the Barents Sea fish community appear to be quite diverse. Interestingly, arctic species show a lower variation in body shapes compared to boreal fish, which present a larger range of PC values for the main shape axes (Fig. 6). The Arctic fish seem to be dominated by eel-like shapes whereas in the south more different shapes are found.

This might reflect differences not only in shape, but also in functional diversity between the two biogeographic areas. Wiedmann (2014) found a much higher functional diversity in the South than in the North of the Barents Sea. His results can be supported by the morphological findings in this study.

4.4. Summary

Finally, the main findings of this study suggest:

- (a) Barents Sea fish differ mostly in anal and dorsal fin location and base-length as well as in overall body shape.
- (b) Through differences in the location and base-length of anal and dorsal fins, diet and habitat differences can be identified. Long-based fins are associated with benthivores living in demersal habitats. Short-based fins are usually presented by planktivorous fish living in pelagic habitats.
- (c) Biogeographic differences can be identified through differences in overall shape. Eel-like, elongated fish are more often found in the arctic environment which might imply an adaptation to life under the ice.
- (d) Large demersals and flatfish with long-based anal and dorsal fins can distribute energy over large temporal and spatial scales and function as links between higher and lower trophic levels.
- (e) Eel-like, elongated fish are very efficient in using locally abundant, benthic resources.
- (f) Migratory species with streamlined bodies and short anal and dorsal fins such as herring and capelin transport energy in the form of resources in time and space throughout the system. Such species are essential for the functioning of an ecosystem and therefore play important key roles.

4.5. Limitations and further advise

This study was the first approach to investigate and identify the shape variation within the Barents Sea fish community and it certainly showed: shape matters!

However, several landmarks were set, though they only took the overall body shape and location of fins insertions into account. This might result in more general conclusions compared to other studies, where for example exact mouth position, intestinal length, dentition and length and area of fins were considered. Additionally, the landmarks do not reflect whether a fish shows one, two or more median fins, and suction cups could not be taken into account either. This limits the interpretation ability on the swimming mode as well as on habitat preferences. Also, flatfish were not clearly reflected as anatomically different through the used landmarks.

However, in this study, a fast and easy applicable approach was chosen and an extension in landmarks and morphometrics might make this more expensive and time consuming. Also, some information might be difficult to obtain, as for example intestinal length, and the method of using almost exclusively internet sources and technical devices might need to be omitted.

Nevertheless, this study still poses an important step towards the identification of shape variation in Barents Sea fish. Ecomorphology resembles an important methodology to better understand shape in regard to function and is starting to find more and more applications. Shape information is frequently being applied now in functional trait matrices (Wiedmann, 2014). This can then be used, for instance, to further examine functional diversity and functional redundancy. With those latest methods, information on ecosystem functioning and its resilience and vulnerability can be obtained (Wiedmann, 2014). Such information is especially needed in times where climate change is posing a constant threat and large fisheries are adding additional pressure to the system. Climate change is predicted to strongly influence species distribution and migration patterns which will result in food web changes, influencing ecosystem functioning (Wassmann, 2011; Wassmann et al., 2006). Therefore knowledge on ecosystem functioning and how it will react to stressors will be necessary in the future for appropriate resource management and sustainable harvest (Wiedmann, 2014).

As a next step I suggest further and more detailed investigations on the ecomorphology of Barents Sea fish to gather higher resolved results. Through additional discriminant analysis certain shape characteristics could be identified that might then allow to class fish into their specific functional groups as established by Wiedmann (2014). By that, more information and further insights on the functioning of the fish community in the Barents Sea could be obtained.

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Appendix

App. 1: Source, type and acknowledgments of fish images which were used for the landmark analysis.

Species	Source	Image type	Acknowledgement
<i>Anarhichas denticulatus</i> (Krøyer, 1845)	Scandfish Poster	Drawing	-
<i>Anarhichas lupus</i> (Linnaeus, 1758)	Scandfish Poster	Drawing	-
<i>Anarhichas minor</i> (Olafsen, 1772)	Scandfish Poster	Drawing	-
<i>Anisarchus medius</i> (Reinhardt, 1837)	Atlas of the Barents Sea Fishes	Photograph	T. de Lange Wenneck
<i>Arctogadus glacialis</i> (Peters, 1872)	Scandfish Poster	Drawing	-
<i>Arctozenus risso</i> (Bonaparte, 1840)	www.marinespecies.org	Photograph	Claude Nozères
<i>Argentina silus</i> (Ascanius, 1775)	Scandfish Poster	Drawing	-
<i>Artediellus atlanticus</i> (Jordan & Evermann, 1898)	www.species- identification.org	Drawing	V. V. Federov
<i>Benthosema glaciale</i> (Reinhardt, 1837)	Scandfish Poster	Drawing	-
<i>Boreogadus saida</i> (Lepechin, 1774)	Scandfish Poster	Drawing	-
<i>Brosme brosme</i> (Ascanius, 1772)	Scandfish Poster	Drawing	-
<i>Careproctus</i> sp. (Krøyer,	Scandfish Poster	Drawing	-

1861)			
<i>Chimaera monstrosa</i> (Linnaeus, 1758)	Scandfish Poster	Drawing	-
<i>Clupea harengus</i> (Linnaeus, 1758)	Scandfish Poster	Drawing	-
<i>Cottunculus sadko</i> (Essipov, 1937)	Scandfish Poster	Drawing	-
<i>Cyclopterus lumpus</i> (Linnaeus, 1758)	Scandfish Poster	Drawing	-
<i>Enchelyopus cimbrius</i> (Linnaeus, 1766)	Atlas of the Barents Sea Fishes	Photograph	Andrey Dolgov
<i>Entelurus aequoreus</i> (Linnaeus, 1758)	Atlas of the Barents Sea Fishes	Photograph	Andrey Dolgov
<i>Eumicrotremus derjugini</i> (Popov, 1926)	Scandfish Poster	Drawing	-
<i>Eumicrotremus spinosus</i> (Fabricius, 1776)	Scandfish Poster	Drawing	-
<i>Gadiculus argenteus</i> (Guichenot, 1850)	Scandfish Poster	Drawing	-
<i>Gadus morhua</i> (Linnaeus, 1758)	Scandfish Poster	Drawing	-
<i>Gaidropsarus argentatus</i> (Reinhardt, 1837)	Scandfish Poster	Drawing	-
<i>Gasterosteus aculeatus</i> (Linnaeus, 1758)	Scandfish Poster	Drawing	-
<i>Glyptocephalus cynoglossus</i> (Linnaeus, 1758)	Scandfish Poster	Drawing	-
<i>Gymnelus</i> sp. (Reinhardt, 1833)	Atlas of the Barents Sea Fishes	Photograph	Andrey Dolgov

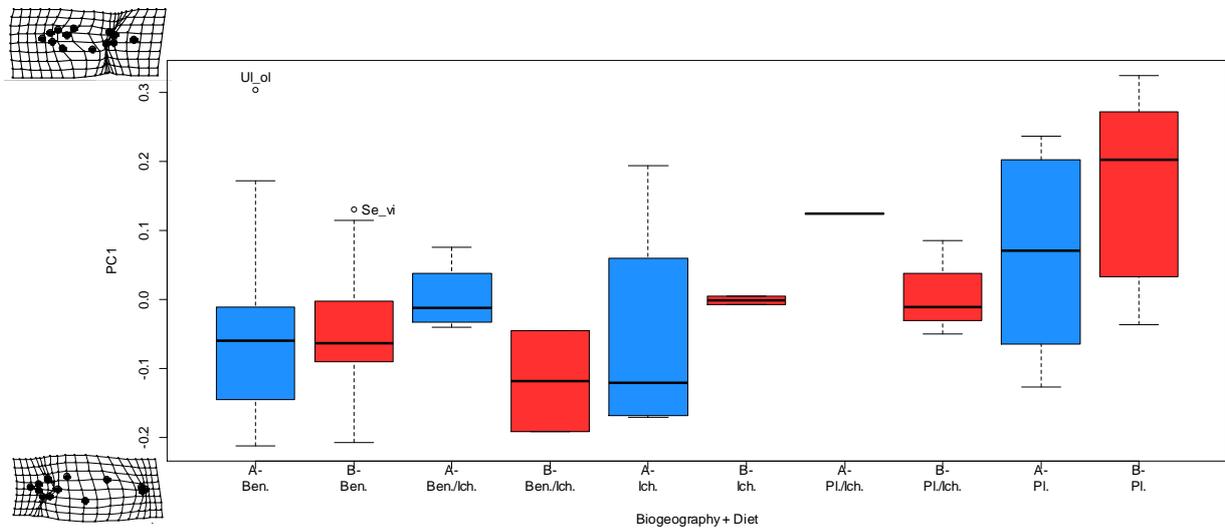
<i>Gymnocanthus tricuspis</i> (Reinhardt, 1830)	www.marinespecies.org	Photograph	Claude Nozères
<i>Hippoglossoides platessoides</i> (Fabricius, 1780)	Scandfish Poster	Drawing	-
<i>Hippoglossus hippoglossus</i> (Linnaeus, 1758)	Scandfish Poster	Drawing	-
<i>Icelus bicornis</i> (Reinhardt, 1840)	www.species-identification.org	Drawing	V. V. Federov
<i>Icelus spatula</i> (Gilbert & Burke, 1912)	www.species-identification.org	Drawing	V. V. Federov
<i>Leptagonus decagonus</i> (Bloch & Schneider, 1801)	Scandfish Poster	Drawing	-
<i>Leptoclinus maculatus</i> (Fries, 1838)	www.species-identification.org	Drawing	V. M. Makushok
<i>Limanda limanda</i> (Linnaeus, 1758)	Scandfish Poster	Drawing	-
<i>Liparis fabricii</i> (Krøyer, 1847)	Atlas of the Barents Sea Fishes	Photograph	Andrey Dolgov
<i>Liparis gibbus</i> (Bean, 1881)	Scandfish Poster	Drawing	-
<i>Lumpenus fabricii</i> (Reinhardt, 1836)	www.species-identification.org	Drawing	V. M. Makushok
<i>Lumpenus lampretaeformis</i> (Walbaum, 1792)	www.species-identification.org	Drawing	V. M. Makushok
<i>Lycenchelys kolthoffi</i> (Jensen, 1904)	Scandfish Poster	Drawing	-
<i>Lycodes esmarkii</i> (Collett, 1875)	Scandfish Poster	Drawing	-

<i>Lycodes eudipleurostictus</i> (Jensen, 1902)	Scandfish Poster	Drawing	-
<i>Lycodes frigidus</i> (Collett, 1879)	Atlas of the Barents Sea Fishes	Photograph	G. Langhelle
<i>Lycodes gracilis</i> (Sars, 1867)	Boat survey	Photograph	Charlotte Weber
<i>Lycodes pallidus</i> (Collett, 1879)	Scandfish Poster	Drawing	-
<i>Lycodes polaris</i> (Sabine, 1824)	www.marinespecies.org	Photograph	Fisheries and Oceans Canada, Claude Nozères
<i>Lycodes reticulatus</i> (Reinhardt, 1835)	Scandfish Poster	Drawing	-
<i>Lycodes rossi</i> (Malmgren, 1865)	www.species-identification.org	Drawing	A. P. Andiashev
<i>Lycodes seminudus</i> (Reinhardt, 1837)	www.species-identification.org	Drawing	A. P. Andiashev
<i>Lycodes squamiventer</i> (Jensen, 1904)	www.species-identification.org	Drawing	A. P. Andiashev
<i>Lycodonus flagellicauda</i> (Jensen, 1902)	www.species-identification.org	Drawing	A. P. Andiashev
<i>Macrourus berglax</i> (Lacepède, 1801)	Scandfish Poster	Drawing	-
<i>Mallotus villosus</i> (Müller, 1776)	Scandfish Poster	Drawing	-
<i>Maurolicus muelleri</i> (Gmelin, 1789)	Scandfish Poster	Drawing	-
<i>Melanogrammus aeglefinus</i> (Linnaeus, 1758)	Scandfish Poster	Drawing	-
<i>Merlangius merlangus</i> (Linnaeus, 1758)	Scandfish Poster	Drawing	-

<i>Micromesistius poutassou</i> (Risso, 1827)	Scandfish Poster	Drawing	-
<i>Microstomus kitt</i> (Walbaum, 1792)	Scandfish Poster	Drawing	-
<i>Molva molva</i> (Linnaeus, 1758)	Scandfish Poster	Drawing	-
<i>Myoxocephalus scorpius</i> (Linnaeus, 1758)	Scandfish Poster	Drawing	-
<i>Paraliparis bathybius</i> (Collett, 1879)	www.species- identification.org	Drawing	D. L. Stein & K. W. Able
<i>Pleuronectes platessa</i> (Linnaeus, 1758)	Scandfish Poster	Drawing	-
<i>Pollachius virens</i> (Linnaeus, 1758)	Scandfish Poster	Drawing	-
<i>Reinhardtius hippoglossoides</i> (Walbaum, 1792)	Scandfish Poster	Drawing	-
<i>Sebastes mentella</i> (Travin, 1951)	Scandfish Poster	Drawing	-
<i>Sebastes norvegicus</i> (Ascanius, 1772)	Atlas of the Barents Sea Fishes	Photograph	T. de Lange Wenneck
<i>Sebastes viviparus</i> (Krøyer, 1845)	Scandfish Poster	Drawing	-
<i>Somniosus microcephalus</i> (Bloch & Schneider, 1801)	Scandfish Poster	Drawing	-
<i>Triglops murrayi</i> (Günther, 1888)	Scandfish Poster	Drawing	-
<i>Triglops nybelini</i> (Jensen, 1944)	www.species- identification.org	Drawing	V. V. Fedorov
<i>Triglops pingelii</i>	www.species-	Drawing	V. V. Fedorov

(Reinhardt, 1837)	identification.org		
<i>Trisopterus esmarkii</i> (Nilsson, 1855)	Scandfish Poster	Drawing	-
<i>Ulcina olrikii</i> (Lütken, 1877)	www.marinespecies.org	Drawing	Duc d'Orléans

App. 2: Box and Whisker plot for the first shape axis (PC1) and the different diet-types in combination with biogeography, with deformation grids of PC1. Mean values are represented by thick black lines within the boxes, and whiskers correspond to minimum and maximum values (where there is no outliers). Outliers marked as dots and labeled with Latin species name abbreviations. **A:** Arctic; **AB:** Arcto-Boreal; **B:** Boreal; **Ben.:** Benthosfeeder; **Ben./Ich.:** Benthos/Ichthyophage; **Ich.:** Ichthyophage; **Pl./Ich.:** Planktonfeeder/Ichthyophage; **Pl.:** Planktonfeeder; **Se_vi:** *Sebastes viviparus*, Norway redfish; **Ul_ol:** *Ulcina olrikii*, Arctic alligatorfish.



App. 3: Map of the Barents Sea with Procrustes transformed species shapes plotted at their mass center of distribution. Labels according to Latin species name abbreviations as listed in Table 1.

