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A morphometric dive into fish diversity

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Abstract. Trait-based approaches are increasingly popular in ecology to describe communities and their responses to natural or anthropogenic changes. Morphology is an integrative trait that combines functional and evolutionary information. However, the objective and quantitative description of the morphological diversity is quite challenging. Modern morphometrics encompass an array of mathematical approaches that turn shapes into quantitative variables. For models with no or only a few homologous points, outline analysis (e.g., elliptical Fourier transform) converts the outline geometry into quantitative variables, which can be used in the multivariate framework. The elliptical Fourier transform here describes the shape of 85 fish species found in the North Sea. This study shows that the main component of morphological diversity in the North sea is the elongation and development of dorsal, pelvic, and caudal fins. The spatial distribution of morphological diversity decreases along a latitudinal gradient, with higher diversity in the southern part of the study area. Compared to species diversity, our results indicate that environmental conditions filter morphological traits in the northern North Sea. Outline analysis is a powerful approach to provide an objective description of fish morphology and to improve our understanding of the diversity of large marine ecosystems.

Key words: elliptical Fourier transform; fish diversity; morphological traits; North Sea; outline analysis.

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INTRODUCTION

Trait-based approaches are increasingly popular in ecology to describe communities and their responses to natural or anthropogenic changes (Keddy 1992, McGill et al. 2006, Mouillot et al. 2013). These approaches characterize species by key features, known as traits, which can be the morphological, biochemical, physiological, structural, phenological, or behavioral characteristics of an organism. Traits help researchers to understand species responses to the environment and the contribution of community biodiversity to the ecosystem functioning (Violle et al. 2007, 2014). Morphology is a highly integrative trait that combines functional and evolutionary

information (Wainwright and Reilly 1994). The high inertial and viscous drag of water (e.g., compared to air) is a major selection pressure on the shape of marine organisms. However, the huge morphological diversity of fishes has often been described subjectively and qualitatively (Pecuchet et al. 2016, Froese and Pauly 2017). But trait-based approaches favor quantitative traits that are considered more practical, objective, and informative than their qualitative counterparts (McGill et al. 2006).

The quantitative description of shapes has long been challenging. Morphometrics, the statistical description of shapes, now distinguishes between traditional and modern morphometrics (Rohlf 1990). Traditional morphometrics rely

upon the measurements of shape indicators such as lengths, areas, angles, and their ratios (Gatz 1979, Wainwright 1988, Wikramanayake 1990), hence focusing on selected aspects of shape only (subjectively chosen and/or technically constrained). Consequently, the original shape cannot be unequivocally reconstructed from the measured indicators. Modern morphometrics, in contrast, consider the entire shape, and two main approaches are currently used: configuration of landmarks and outline analysis (Rohlf 1990, Claude 2008, Bonhomme et al. 2014). The first approach uses homologous points between shapes, known as landmarks, and studies their relative position. The technique has been used extensively in the last decades to study intra-species fish morphology (Loy et al. 2000, Klingenberg et al. 2003, Costa and Cataudella 2007, Elmer et al. 2010). However, homologous points are often hard to define between various shapes—for example, between species from different families, and the number and position of homologous landmarks vary between studies and organisms (Farré et al. 2016). In contrast, outline analyses consider the whole outline. The most popular outline analysis approach is elliptical Fourier transform (EFT), and it has been used in marine biology to describe otolith shapes (Tracey et al. 2006, Mérigot et al. 2007), shells (Costa et al. 2008), and fish species morphologies (Loy et al. 2000, Ventura et al. 2017). To our knowledge, these studies considered very similar biological objects only and the technique was never extended to explore the diversity patterns in species assemblages.

Using the North Sea as a case study, this study demonstrates the use of EFT to quantitatively describe the morphological variability in a highly diverse marine fish species assemblage (Daan et al. 1990). The North Sea fish community is structured along a strong latitudinal gradient, mainly associated with differences in depth and primary production (Emeis et al. 2015, Frelat et al. 2017). The many commercially important fish populations provide highly valued ecosystem services. Our new quantitative description of morphological variability can improve our understanding of the community diversity and identify environmental processes structuring the fish community of this large marine ecosystem.

MATERIALS AND METHODS

Sample collection

Images of bony fishes from the North Sea were collected in January 2017 from nine online image databases (Appendix S1). Four criteria were used to only retain comparable images: (1) lateral views of (2) male individuals (to cope with any sexual dimorphism) (3) with all their fins well represented (i.e., spread and not eaten), and (4) no eel-shaped species (discarded because of their recurrent serpentine representation). We considered images of all species recorded regularly during bottom trawl survey in the North Sea and fitting the four criteria previously cited. When available, several images of the same species were included to evaluate the robustness of the approach. A total of 218 images (48 photographs and 170 drawings) from 85 bony fish species of the North Sea were included in this study (Appendix S1).

Before performing the outline analysis, we transformed the images into black silhouettes (Fig. 1b). Numerous studies have defined landmarks on fish to study their morphology. We used five commonly used landmarks (Loy et al. 2000, Elmer et al. 2010, Farré et al. 2016) that are located on the outline, easily recognizable, and present on all species: (1) snout tip; (2) anterior insertion of the dorsal fin; (3) dorsal and (4) ventral insertion of the caudal fin; and (5) insertion of the pelvic fin (Fig. 1b). The silhouettes were then converted into $(x; y)$ coordinates.

Elliptical Fourier transform

Elliptical Fourier transform is a popular method of outline analysis, fitting separately the x and y coordinates of an outline projected on a plane (Rohlf 1990, Bonhomme et al. 2014). Before conducting such analysis, outlines must be aligned to remove differences in rotation, translation, or size. We used five landmarks to align the outlines using a full Procrustes superimposition. This superimposition optimally rotates, translates, and scales these five landmarks to minimize Procrustes distances between them. The first landmark (position of the mouth) was defined as the starting point of every outline. Outlines are closed curves than can be described as periodic functions. The EFT describes the outline geometry as two periodic functions—the difference between the abscissa/ordinate of the first and all successive points (Fig. 1c). The Fourier

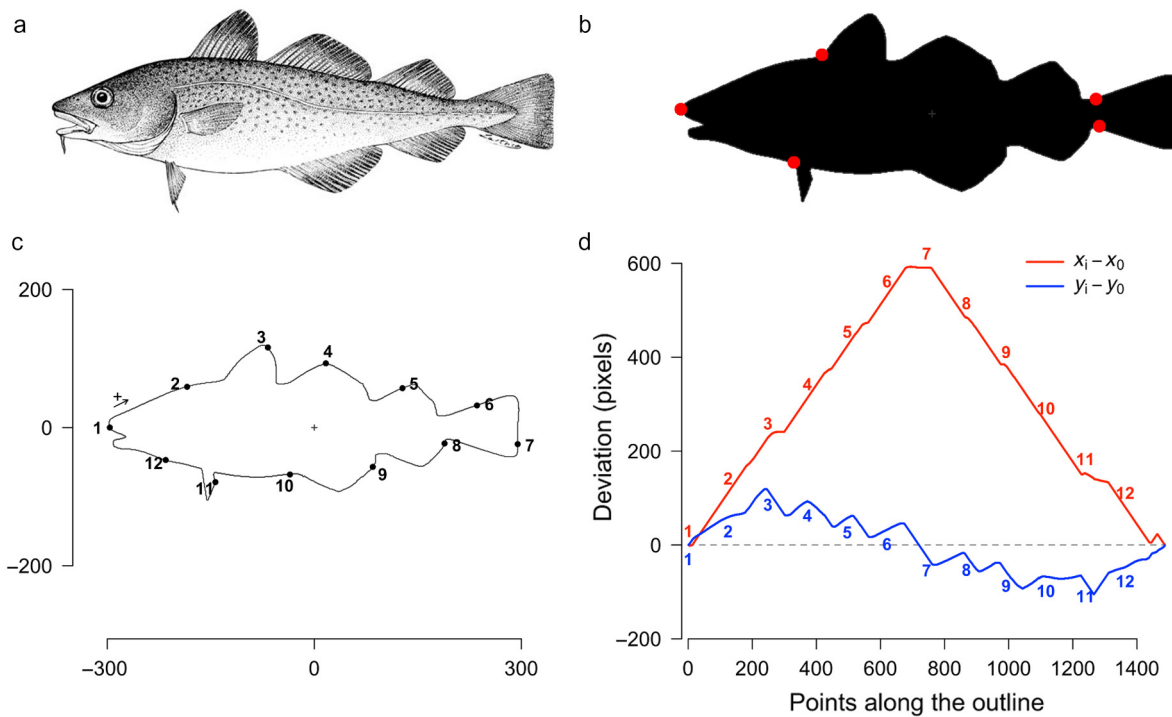


Fig. 1. Illustration of outline analysis using elliptical Fourier transform (EFT). From original image (a), to black silhouette with five landmarks (b), on which the outline (c), can be described with EFT (d). The species in the figure is *Gadus morhua*, image from FAO.

transform then decomposes them into a harmonic sum of trigonometric functions, weighted with coefficients known as harmonic coefficients. The original signal f can then be expressed as follows:

$$f(t) = \frac{a_0}{2} + \sum_{n=1}^{+\infty} \left[a_n \cos\left(n \frac{2\pi}{T} t\right) + b_n \sin\left(n \frac{2\pi}{T} t\right) \right] \tag{1}$$

with T as the perimeter of a given closed outline and t as the curvilinear abscissa that varies from 0 to T . The harmonic coefficients a_n and b_n can be expressed as follows:

$$a_n = \frac{2}{T} \int_0^T f(t) \cos\left(n \frac{2\pi}{T} t\right) dt$$

$$b_n = \frac{2}{T} \int_0^T f(t) \sin\left(n \frac{2\pi}{T} t\right) dt. \tag{2}$$

Four coefficients are obtained for each harmonic calculated. The number of harmonics was chosen to retain 99% of the cumulative harmonic power. The harmonic coefficients can be considered as

quantitative variables and analyzed within a multivariate framework. More details can be found in Bonhomme et al. (2014). A principal component analysis (PCA) was calculated on the matrix of coefficients. Each principal component (PC) captured an independent and synthetic aspect of shape variability. Morphospaces, theoretical shapes regularly drawn on the factorial plane, helped to interpret the results. The first three PCs were compared to commonly used morphological traits by categorizing the caudal and body shapes (Pecuchet et al. 2016, Dencker et al. 2017; Appendix S2: Text S1). Finally, we compared the morphological distance (Euclidean pairwise distances of images calculated from coordinates on the first three PCs) with the taxonomical distance calculated with five taxonomic levels (Appendix S3: Text S1).

Morphological diversity in the North Sea

Abundance data of the North Sea fish community has been collected by the North Sea International Bottom Trawl Survey (ICES 2015), an international effort to monitor demersal fish

populations. The sampling procedure monitored the North Sea on a regular grid of 1° longitude \times 0.5° latitude, known as the ICES rectangles. Each contributing research vessel applies a standard otter trawl net which is hauled over the seabed for 30 min. The data for the first quarter of the period 2006–2015 were downloaded from <http://datras.ices.dk/>. To avoid any bias that may arise due to different sampling efforts (i.e., different number of hauls per ICES rectangles), 10 hauls per ICES rectangles were randomly selected, and we assessed their species and morphological richness. We repeated the random selection 100 times to estimate the variability of species occurrence (i.e., the presence or absence of species). ICES rectangles with <10 hauls in the 10-yr period were removed from the analysis. In total, 172 ICES rectangles were included in the analysis.

Two indicators of morphological diversity were calculated for each ICES rectangle from occurrence data and the mean scores of species on the three PCs defining the morphospace (Villéger et al. 2008). Morphological richness is the volume of the morphospace occupied by the convex hull of the community. Morphological dispersion is the mean distance to the barycenter of each community (Laliberté and Legendre 2010). The morphological diversity was then compared to species (i.e., taxonomic) richness obtained from the occurrence data. We expected that the morphological richness increases with taxonomic richness. A null model for the relationship between species and morphological richness was estimated by randomly selecting a given number of species from the entire species pool (with specific probabilities in accordance with their occurrence in the North Sea) and by calculating the morphological diversity indicators with a random assemblage of species. We repeated the randomization process 1000 times and computed it for species richness ranging from 10 to 50.

Software and tutorial

All statistical analyses were conducted in the programming environment R 3.3 (R Core team 2017). Morphometric analyses were done with the package Momocs 1.2.3 (Bonhomme et al. 2014), while morphological diversity indicators were calculated with the FD package. The

geographic distribution of species and morphological richness was visualized with the mapdata and rgdal packages. A tutorial explaining the EFT on fish communities is available on GitHub: <https://rfrelat.github.io/FishMorpho.html> (<https://doi.org/10.5281/zenodo.1108518>).

RESULTS

Outline analysis and morphological space

Fourteen harmonics were enough to gather 99% of the total harmonic power (Fig. 2). The PCA on the 56 resulting coefficients yielded three PCs, accounting for 78% of the variance (Fig. 3). The first principal component (PC1), accounting for 42% of the total variance, highlighted the general rounding or elongation of the shapes (Fig 3b). Shapes presenting the lowest scores on this PC belonged to elongated fish species such as the smooth sandeel (*Gymnammodytes semisquamatus*) and the great sandeel (*Hyperoplus lanceolatus*). On the other hand, shapes presenting the highest values on this component belonged to flat fish species such as the turbot (*Scophthalmus maximus*) or the European plaice (*Pleuronectes platessa*).

The second principal component (PC2), explaining 24% of the variability, highlighted the

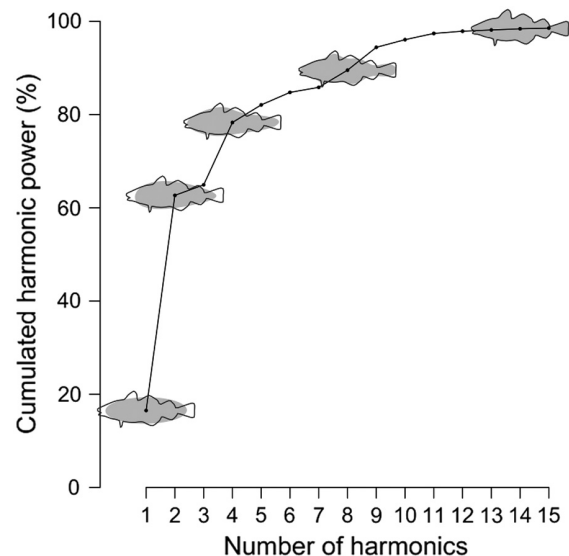


Fig. 2. Progressive reconstruction of shapes. Fourteen harmonics gathered 99% of the total harmonic power.

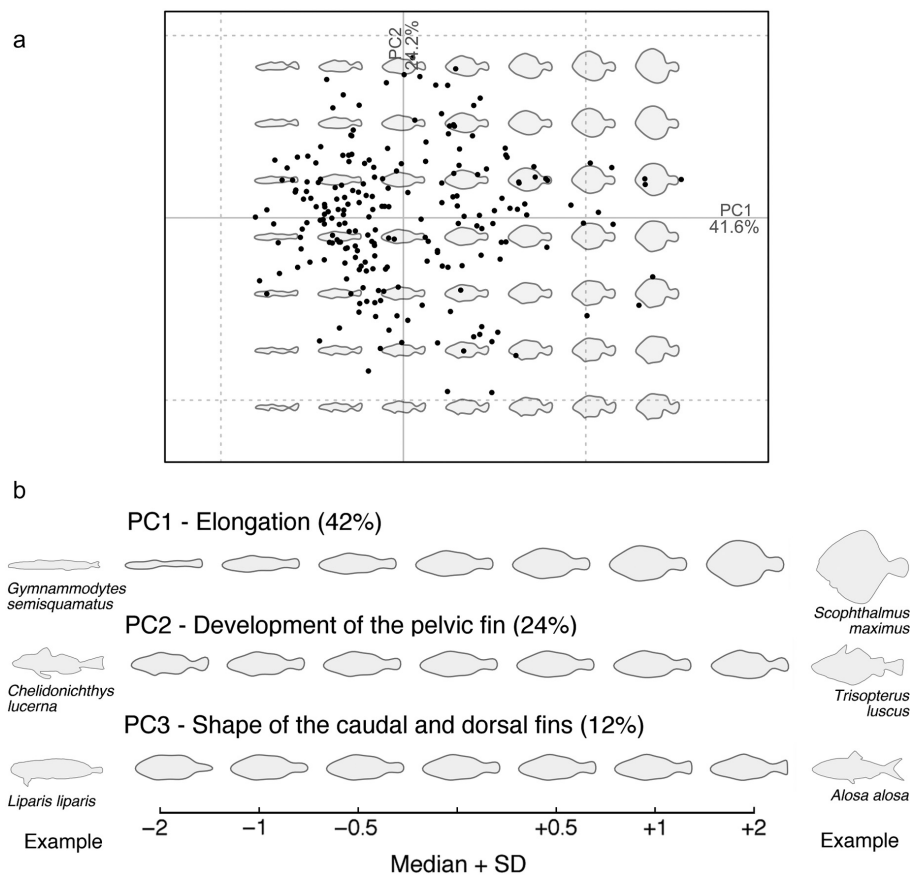


Fig. 3. Principal component (PC) analysis calculated on the matrix of Fourier coefficients. (a) Scatterplot of the scores on the first two PCs, accounting for 66% of the total variance; the morphospace in the background presents theoretical shapes reconstructed from the PCs. (b) Illustration of the synthetic components of shape captured by the first three PCs. Raw outlines of the species projected near PCs extrema are displayed as example.

development of the pelvic fin and the underside. Shapes presenting the lowest values on this component belonged to species with strong and developed pelvic fins such as the tub gurnard (*Chelidonichthys lucerna*) and the golden redfish (*Sebastes norvegicus*). On the contrary, shapes presenting the highest values on this component belonged to species with smooth ventral sides and short pelvic fins such as the Norway pout (*Trisopterus luscus*) and the sand sole (*Pegusa lascaris*).

Finally, the third principal component (PC3), explaining 12% of the variability, was related to the shape of the dorsal and caudal fins. Shapes that presented the lowest values on this component belonged to species with strong, short, and developed dorsal fins and fork-shaped caudal fins such as the Clupeidae family like the allis shad (*Alosa*

alosa), sardine (*Sardina pilchardus*), and herring (*Clupea harengus*). On the other hand, shapes presenting the highest values on this component belonged to species with a continuous body, long dorsal fins, and round-shaped caudal fins such as the striped seasnail (*Liparis liparis*) and the checker eelpout (*Lycodes vahlii*). Body and caudal shape traits described by Pecuchet et al. (2016) were significantly linked with PC1 and PC3, respectively (Appendix S2: Fig. S1). The morphological distance between individuals increased with the taxonomical distance (Appendix S3: Fig. S1). We found no significant difference in the distances within species if calculated only with the same type of images, or with one drawings and one photograph (*P*-value of the Student's *t* test = 0.26). This result indicated that the type of images does not

influence our analysis. The average scores for each species on the three components are provided in Appendix S4.

Morphological diversity in the North Sea fish assemblages

Morphological diversity, expressed as richness or dispersion, decreased along a latitudinal gradient with highest values in the southern North Sea (Fig. 4a, b). The maximum morphological diversity was observed in the Kattegat, at the Elbe river mouth, and at the connection to the English Channel. The Kattegat also presented the maximum species richness of all ICES rectangles (39 species recorded). As expected, a positive correlation was found between the species richness and the morphological richness in the null model (Fig. 4c). We compared the observed morphological diversity indicators of each ICES rectangle with their expected values in the null model (Fig. 4c, d). As expected, the null model predicted that morphological richness increased with the number of species (Fig. 4c). Morphological dispersion was not linked with species richness, but the variance of the predictions of the null model decreased with the number of species (Fig. 4d). Most of the area in the northern North Sea had lower morphological richness than predicted by the null model, and nine ICES rectangles had significantly (P value < 0.05) lower morphological richness than expected by the 1000 randomizations in the null model (Fig. 4e). In the southern North Sea, most of the rectangles had morphological richness falling within the range or slightly higher than the predicted level, but none was significantly different those in the null model. Similar patterns were found with morphological dispersion. Eight ICES rectangles in the southern North Sea had significantly higher morphological dispersion than expected, and 12 ICES rectangles located in the northern North Sea had significantly lower morphological dispersion than expected (Fig. 4f).

DISCUSSION

Outline analysis appeared to be effective at describing the morphological diversity of fish species in the North Sea. Elliptical Fourier transform revealed three main components of morphological diversity in marine fish species. The

most important component was related to elongation of the main body; the second to the development of the pelvic fin; and the third to the shape of the dorsal and caudal fins. These three integrative and quantitative variables are good candidates for new morphological traits in accordance with the criteria stated by McGill et al. (2006): “To be useful to community ecology, traits should vary more between than within species and preferably be measured on continuous scales.”

Morphological traits found in this study had already been described by previous subjective and qualitative descriptions (Pecuchet et al. 2016). Furthermore, we found elongation to be the major source of variability in shape, in accordance with numerous studies on fish morphology (Elmer et al. 2010, Claverie and Wainwright 2014, Ventura et al. 2017) and, more generally, on vertebrate morphology (Collar et al. 2013). These similarities suggest that EFT can describe both quantitatively and objectively the known morphological features and reveal more subtle components of morphological diversity. Additional studies should link these morphological traits with specific functions of fish, such as swimming performance and feeding behavior (Norton et al. 1995, Bejarano et al. 2017).

Morphological diversity decreased along a latitudinal gradient with highest values in the southern North Sea. This shallow area is known to host a different species assemblage than the northern part due to different environmental pressures—for example, higher temperature and primary production (Daan et al. 1990, Frelat et al. 2017) and different epibenthic invertebrate community (Callaway et al. 2002). One of the main differences in species assemblages is the numerous small flatfish species that inhabits only the southern North Sea (Callaway et al. 2002). Adding quantitative morphological traits will help researchers to determine the community assembly rules, the relationship between taxonomic and functional diversity (Bellwood et al. 2002, Dencker et al. 2017). As expected, we observed that areas with high species richness were more likely to present a higher morphological richness. However, areas with low species richness in the northern North Sea presented significantly lower morphological diversity than expected, if the species were chosen randomly. This result suggests that the

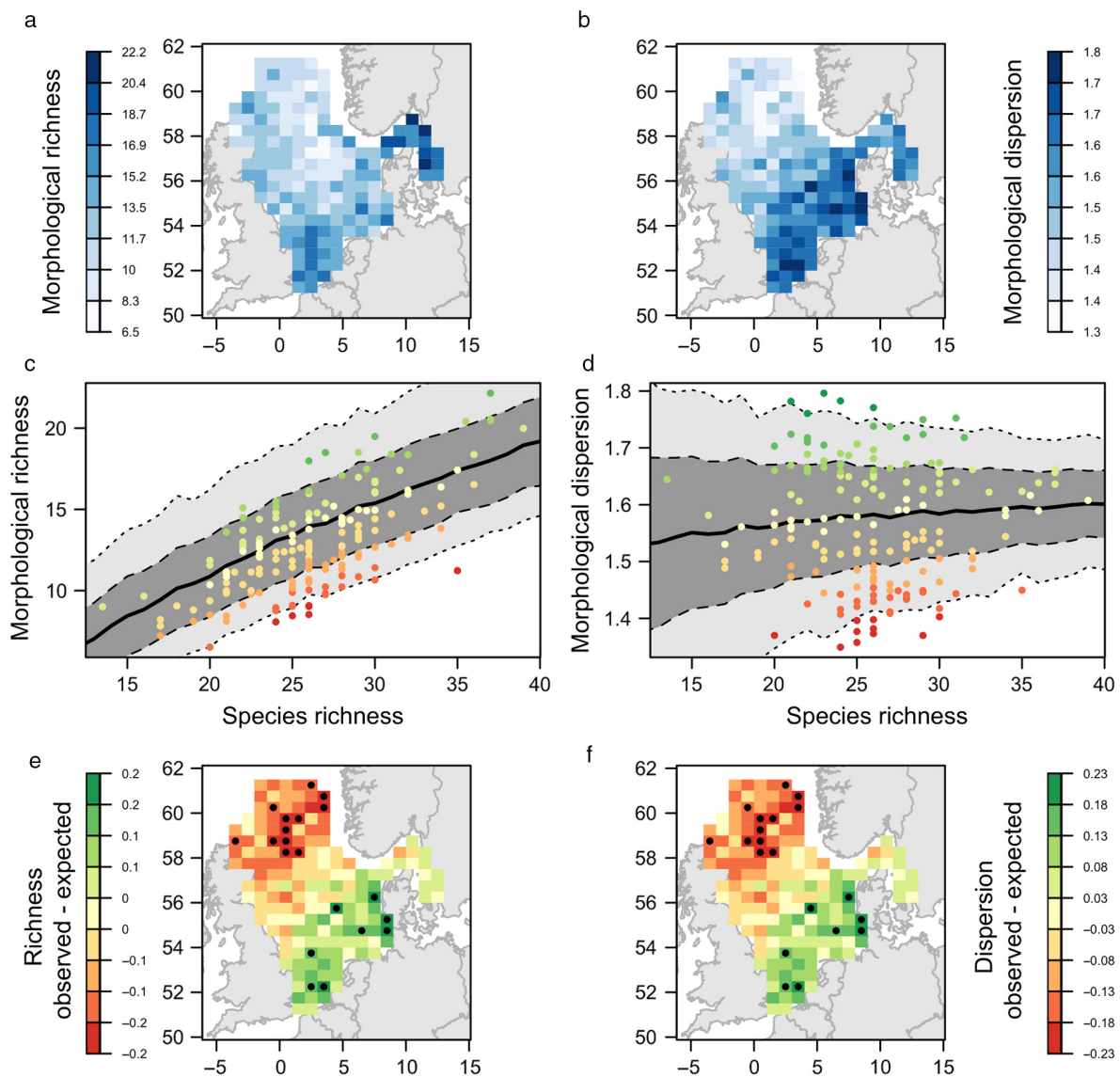


Fig. 4. (a, b) Spatial patterns of fish morphological diversity in the North Sea. (c, d) Relationship between the observed morphological diversity and species richness. The bold black line represents the mean morphological diversity of 1000 random samplings for a given number of species; the shaded areas in dark and light gray represent the standard deviation and 95th percentile, respectively. (e, f) The map of the residuals between observed and predicted morphological diversity. Black dots indicate communities significantly different from the null model. The left column (a, c, e) represents morphological richness, and the right column (b, d, f) represents morphological dispersion.

environmental conditions filter species lacking a specific combination of morphological traits (Keddy 1992, Moullot et al. 2007). This observation was confirmed by morphological dispersion which showed a strong latitudinal gradient and suggests two opposing mechanisms:

environmental filtering in the north and limiting similarity in the south. The border between the two mechanisms matches the boundary between the thermally stratified waters of the northern North Sea and the permanently vertically mixed waters of the southern North Sea (Callaway et al.

2002). The high seasonal fluctuations in bottom water temperature in the south may be a factor limiting the morphological similarities between species, while the more stable conditions in the northern North Sea seem to filter morphologically similar species. This interpretation remains to be confirmed and tested in other large marine ecosystems.

Elliptical Fourier transform is known to be sensitive to the choice of the alignment method but our analysis consistently found the same three main components (Appendix S5). Naturally, fishes are 3D objects whose morphological descriptions could be refined, for example, with EFT on 2D orthogonal views to characterize the cross-section body shape (Terral et al. 2004, Bonhomme et al. 2015, Bouby et al. 2016). It would require a collection of images of the cross-section data for numerous fish species that are not available online yet. Our study focused on only the shape, which is the form minus size, and the latter would probably be an informative covariate. Moreover, the outline analysis produced here only considers the information included in the outline, missing, for example, the shape and the position of the pectoral fin, the operculum, and the eye, features known to have a functional role (Klingenberg et al. 2003, Mouillot et al. 2007, Farré et al. 2016). However, a comparison of landmark-based approach and outline analysis showed no significant differences (Loy et al. 2000) and a recent study shows that most of the morphological variability in reef fishes was found in body elongation (Claverie and Wainwright 2014). The outline analysis of the shape of the single lateral view proved to bring important insights into the diversity of fish morphology. The outcome of the outline analysis can be of great interest for further morphological studies and trait-based approaches in ecology and biogeography. Extending such an approach to the species from other large marine or freshwater ecosystems would characterize the global spectrum of fish morphology.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2220/full>