Guide pratique

Identification of fishes by their otoliths in 3D

English Channel and North Sea

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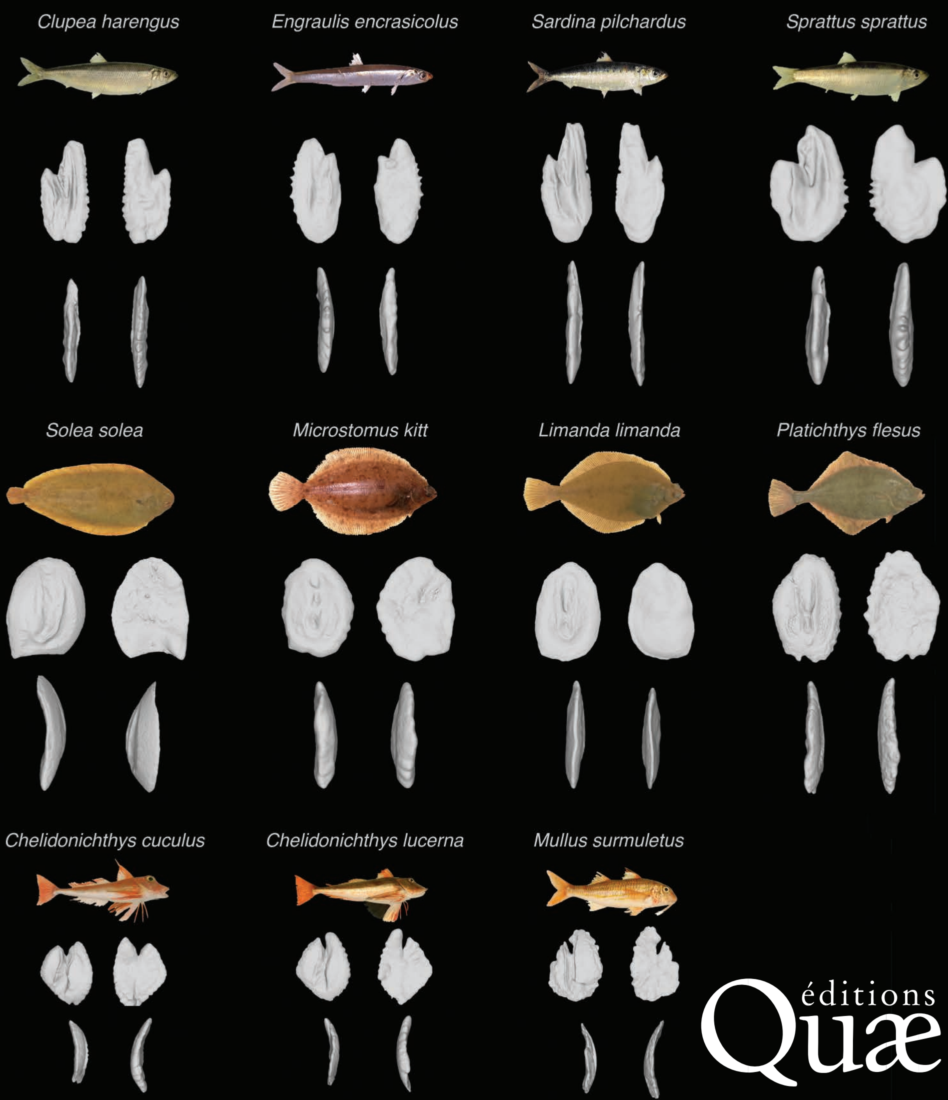

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Content

Introduction

This identification guide to the main fish species of the English Channel and the North Sea covers 22 species. It is intended as an educational tool for students and the general public, and as a reference tool for scientific research studying the otoliths of these species, for example in archaeology, or for identifying the fishes present in the stomach contents of all species that eat fish (seals, birds, fish, etc.).

Study area

The English Channel and the North Sea form a strategic region in North-West Europe from a socio-economic and ecological point of view[1]. This is an important economic zone, with a wide range of human activities, including tourism and leisure, international ports and freight, and the exploitation of living and non-living resources. This maritime area carries almost 20% of the world's traffic, making it one of the busiest in the world. It harbours huge reserves of marine aggregates (sand, gravel) and gas, which resources are coveted by many industries. Other human activities are also developing around marine renewable energies, such as offshore wind and tidal turbines.

The Channel and the North Sea also support a very significant commercial fishing industry, both in terms of the quantity of fish and the number of species exploited. Of the 120 species identified in this region, around 20 account for almost all of the commercial species.

Uses of otoliths in fisheries science

Fish populations are monitored every year to achieve the Maximum Sustainable Yield (MSY) required for a sustainable Common Fisheries Policy into the future. The statistical models used to monitor fisheries therefore require knowledge of the age structure of each management unit, known as a stock, and to assess the limits of each of these stocks (Cadrin and Dickey-Collas, 2015). Calcified parts (scales, vertebrae, fin rays, otoliths, etc.), which grow by successive concentric periodic accretion, are used to determine age. Of these calcified parts, only the otoliths, located in the inner ear cavity, are metabolically inert, i.e. they cannot be altered or resorbed (Casselman, 1987). Furthermore, observation of otolith internal structure shows that they develop according to a periodicity of calcium carbonate deposits ranging from daily to yearly.

The ears (right and left paired structures located on either side of the brain) are made up of a network of canals that connect three cavities (called otic sacs). This entire system is filled with a liquid called endolymph (Panfili *et al.*, 2002).

1. For more information on the area and the development of human activities, please refer to the strategic document for the Channel East-North Sea coastline finalised by France: https://www.dirm.memn.developpement-durable.gouv.fr/IMG/pdf/straegie_de_facade_maritime_memnor_synthese.pdf (consulted on 20/07/2025).

Otoliths are concretions formed largely of calcium carbonate that are present in each cavity. The largest of the cavities contains the largest otolith, called the *sagitta*. The *sagitta* is used for virtually all studies, and is thus the otolith presented in this book. The otolith exists in the otic cavity, and is connected to the brain by a membrane called the *macula* (Panfili *et al.*, 2002). This membrane is in contact with the otolith on its proximal surface (inner surface) in a groove called the *sulcus acusticus* (Figure 1). The *sulcus acusticus* is divided into three parts along an anteroposterior axis, with the *excisura* (the zone delimited by the *rostrum* and the *antirostrum*), the *ostium* and the *cauda*. The characteristics of this zone are closely linked to acoustic development (detection of sound waves) and angular development (detection of accelerations enabling the individual to balance). The shape of the otolith, although very different from one species to another, generally shows a convex proximal inner surface and a concave distal outer surface. Positioned on the inner face, the development of the otolith is often greater on the antero-posterior axis (where the length of the otolith is measured) than on the dorso-ventral axis (where the width of the otolith is measured) (Figure 1).

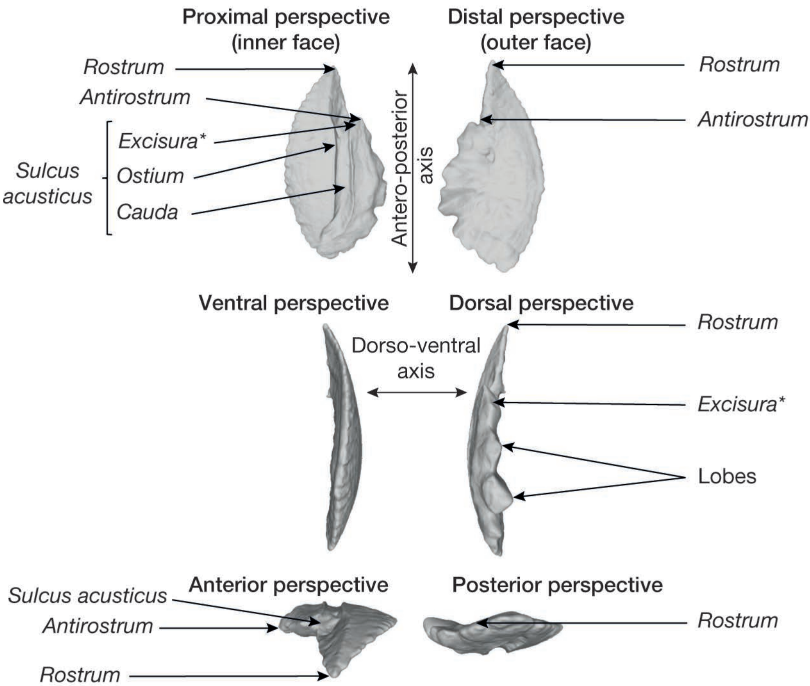


Figure 1. Presentation of a right otolith from the different perspectives extracted from a three-dimensional image.

* *Excisura*: notch separating the *rostrum* from the *antirostrum*.

Otoliths, which evolve throughout the life of a fish, have chemical and physical signatures that correspond to the biological and environmental conditions in which the fish has lived (Casselman, 1987). It was not until the end of the 19th century that scientists observed these otoliths and counted periodic growths on their external surface, making it possible to estimate the age of the fish (Reibish, 1899). Since then, the scientific use of otoliths has continued to grow.

While age and growth are the primary information to be extracted from otoliths, much other scientific research uses the shape and chemical composition of the otolith to discriminate between populations within a species or to trace the geographical movements of individuals. There is also a significant relationship between the growth of fish and that of their otoliths (Lagardère and Troadec, 1997; Fossen *et al.*, 2003; Mahé *et al.*, 2017). By measuring an otolith of a fish, it is therefore possible to estimate the size of the individual to which it belonged. Campana and Thorrold (2001) estimated that nearly 800,000 otoliths were used worldwide in 1999 alone to determine the age structures of commercial fish species, representing a sum of around 8 million Canadian dollars. Similarly, in 2010, 759,403 calcified parts were supplied by various countries to monitor stocks in European waters (ICES, 2011). Every year, more than a million calcified samples, mainly otoliths, are analysed worldwide.

The use of the external shape of the otolith within a species has been developed strongly in research to better understand fish populations and their geographical limits. This shape incorporates all of the variations in environmental conditions and climatic forcing during the life of the fish, alongside the genetic characteristics of the parents. Differences in otolith shape can therefore be attributed to geographical differences linked to the metabolic activity of the organisms, itself being the result of environmental factors and genetic components specific to each individual (Gauldie and Nelson, 1990; Smith, 1992; Begg and Brown, 2000). This use of otolith shape as a method of discriminating between stocks has developed since the 1990s, in particular with the studies by Pontual and Prouzet (1987) and Campana and Casselman (1993). Since then, scientists have developed a keen interest in using otolith shape as a tool for discriminating between fish stocks, with nearly 50 scientific articles published each year over recent years. Annual monitoring by a group of international experts (the Stock Identification Methods Working Group, set up by the International Council for the Exploration of the Sea, ICES) shows that otolith shape analysis is becoming the main method used to define and validate stock limits, ahead of genetic analysis. This predominance can be explained by recent advances in image analysis and data processing, in particular with the development of statistical tools such as R (R Core Team, 2023), or Shape (developed by Iwata and Ukai, 2002). These tools make it possible to carry out studies in larger numbers and at lower cost than the genetic tracer approach, while showing generally comparable results. Since the early 1980s, otoliths have also been used to understand the ecology of fish, based on their chemical composition. Otolith chemistry reflects both exogenous factors (water chemistry, depth, temperature, trophic availability, stress factors, chronic or accidental pollution, etc.) and endogenous factors (ontogeny, metabolism, reproduction, health, etc.) (Radtke and Shafer, 1992). By comparing the chemistry of the otolith with the chemical composition of the water in different places, it is possible to retrace the geographical route taken by the fish during its life, with understanding of the time spent in each place, if the chemical compositions are sufficiently distinct.

1. Species differentiation by otolith morphological characteristics

The external shape of otoliths makes it possible to identify the different fish species to which they belong. Analyses of shape are used in archaeological studies (Disspain *et al.,* 2016; Agiadi, 2022) or targeted at prey-predator relationships within a food web (Lowry, 2011; Stock *et al.,* 2021; Quigley *et al.,* 2023). Between species (i.e. at the interspecific level), there is no link between the size of individuals and the size of their otoliths (Campana, 2005). For example, pelagic fishes[2] such as tuna or swordfish may have small otoliths, while some small reef species may have large otoliths (Campana, 2005). Similarly, fast swimming fishes tend to have more elongated otoliths than those of bentho-demersal species[3] (Volpedo *et al.*, 2008; Tuset *et al.*, 2015).

The external shape of a fish changes from egg to adult. Its morphology therefore changes over the course of its life. This developmental process is called ontogeny. While genetic and environmental factors are sources of explanations for the shape of the otolith, the principle of ontogeny also plays a role. For the same individual, the shape of the otolith evolves over the course of its life, thus the life stage must be taken into account. In this book, several individuals of each species, distributed along a gradient of sizes observed in the natural environment, covering the different life stages (juveniles, young adults, adults who have already reproduced, etc.) are presented and analysed (Figure 2).

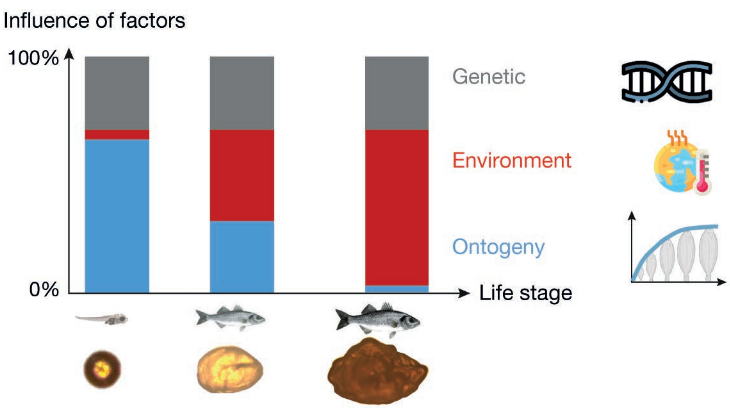


Figure 2. Influence of potential factors (ontogeny, environment, genetic inheritance) on the shape of the fish and its otolith at each life stage.

2. Pelagic fish live mainly at the top of the water column, close to the surface.
3. Benthic species live at the bottom of the water column, i.e. close to the bottom, and feed mainly on animals in or on the bottom. Bentho-demersal species live close to the bottom, but may also spend part of their time in the middle of the water column.

Choice of species and harvesting

Only around 20 of the 120 species identified in the Channel and North Sea are currently exploited commercially, therefore the 22 most commercially exploited fish species were selected for this guide, taking three to five individuals per species for comparison of otoliths within or between species. The choice of the number of individuals enables the entire size range of each species to be accurately represented. For the adult stages, we discuss individuals of different sizes, without differentiating males and females. Among the species, there are two different morphotypes: flatfish, which interact strongly with the bottom, and roundfish, which interact less strongly with the bottom. In addition, these species live differently in the water column: some are pelagic and others benthic. All samples were taken by the Ifremer Institute, in particular by the team from the Channel and North Sea Fisheries Unit, during scientific campaigns carried out on the oceanographic vessel Thalassa. These samples were taken in the Channel and the North Sea as part of the international monitoring of fish populations to assess the state of health of commercial fish populations. Two scientific campaigns conducted by Ifremer each year for France covering the Channel and North Sea were used: the International Bottom Trawl Survey (IBTS, in January and February) and the Channel Ground Fish Survey (CGFS, in September and October).

Methodology

3D image acquisition

General principle of X-ray microtomography

The technique used to acquire images of the various otoliths is called X-ray microtomography[4]. This is a non-destructive and non-invasive technique used to characterise the microstructure of dense and porous materials. The technique is used in a variety of sectors, including medicine, materials, archaeology and the food industry. X-ray microtomography provides access to the 3D geometry of a sample from images acquired in 2D. The device acquires multiple X-ray images when the object is rotated a certain number of revolutions. Reconstruction software then transforms the 2D images into a 3D volumetric image.

Figure 3 shows the principle of X-ray microtomography acquisition. The sample is placed in the acquisition chamber and X-rays pass through the sample. Depending on the density of the sample, these rays are attenuated to a greater or lesser extent and are collected at the output by a detector, which produces an X-ray image of the sample. By rotating the sample, it is possible to acquire multiple X-rays taken from different angles.

Microtomography acquisition is defined according to a number of specific parameters.

The voltage (in kilovolts) and current (in milliamperes) parameters of an X-ray generator control the maximum energy and quantity of X-ray photons emitted by the source. The power of the X-rays emitted is determined by the voltage/current combination as a function of the density of the sample. The greater the density, the greater the power of the X-rays required to detect the object with the sensor.

4. The term "microtomography" comes from the X-ray source, a sealed tube with a focal spot of the order of a micrometre in diameter.

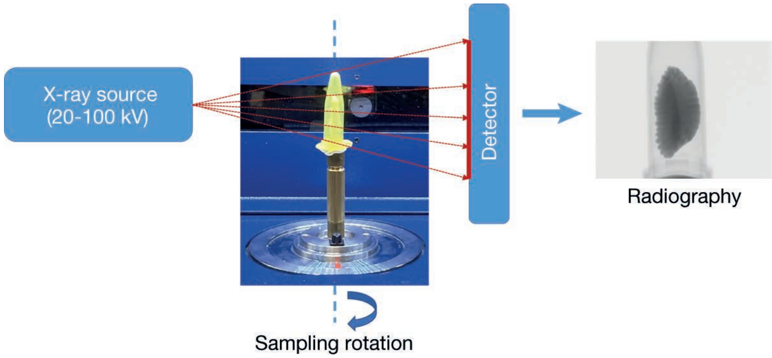


Figure 3. Schematic diagram of the principle of X-ray microtomography.

A filter can be positioned between the source and the sample to harden the X-ray beam. The filter eliminates the lower-energy photons and retains the higher-energy photons, which are better able to pass through the sample. It can be made of aluminium or copper, for example. The choice of whether or not to use a filter depends on the density of the sample. Dense samples are difficult for X-rays to penetrate, so it is necessary to increase the power. However, if the power of the X-rays is high, the detector receives too many photons (which are not absorbed by the object), creating noise in the image. By eliminating the lower-energy photons, the spurious photons will not be detected and the image will be less noisy. The use of filters is therefore recommended when samples are dense. On the other hand, the use of filters implies an increase in exposure time, and therefore in acquisition time. The rotation step of the sample is the degree of rotation that the object undergoes between each radiographic exposure. This angle, together with the number of revolutions of the sample, also determines the image acquisition time (which can range from a few minutes to several hours). For example, if a rotation step of 0.2° is chosen with a total rotation of 360°, 1,800 radiographs of the sample will be acquired (one every 0.2°), or half as many if a rotation of 180° is chosen. Nevertheless, even if the acquisition time is longer, a 360° rotation over the entire sample provides better 3D image reconstruction for a heterogeneous sample. A compromise between image quality, detail and acquisition time was reached for each species (see Appendix).

The nominal resolution, expressed in voxels[5] or micrometres, defines the minimum size of the observable elements of the object (for example, if the nominal resolution is 10 µm, no element smaller than 10 µm can be observed). The nominal resolution applied depends on the size of the sample. The smaller the sample, the closer to the source it can be observed, and the better the nominal resolution.

Once the acquisition is complete, image reconstruction software is used to generate virtual 2D sections of the sample from the X-rays. A stack of 2D sections is thus obtained. These virtual sections contain the density information of the sample in levels of grey. From this stack of sections, another software program is then used to construct a 3D image in volume rendering (Figure 4). Note that the 3D images obtained at this stage only provide a 3D visualisation of the scanned sample, and that additional steps (see Segmentation, *infra*) are required to obtain 3D images that can be used to characterise the morphology of the objects studied.

5. Voxel: unit of size in 3D imaging. It is the equivalent of a pixel in 2D imaging.

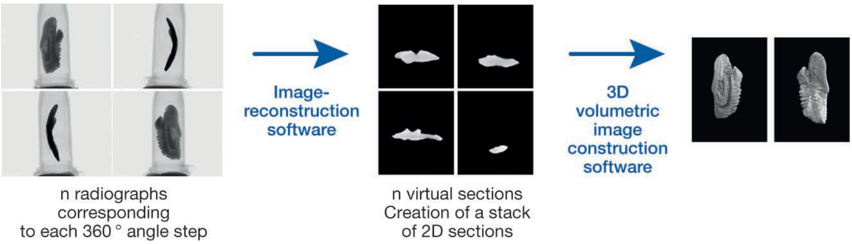


Figure 4. Schematic showing the reconstruction of images acquired by X-ray microtomography.

Otolith image acquisition equipment

The list below provides a non-exhaustive overview of the X-ray microtomography equipment that can be used to scan otoliths. This list has been compiled from the equipment owned by the laboratories participating in the study presented in this book.

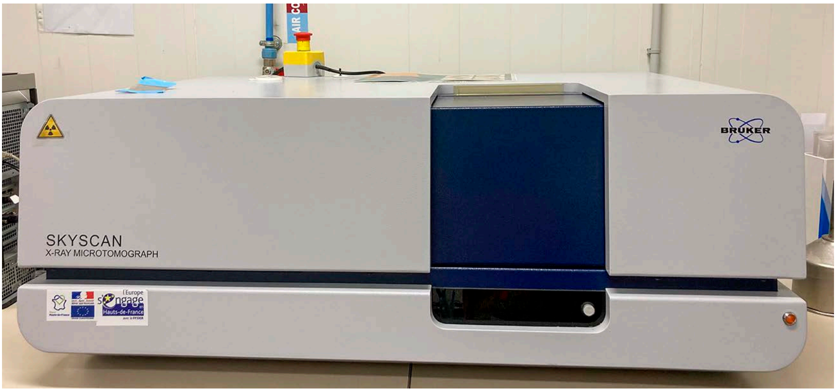
Skyscan 1174 from Bruker

Since 2014, the UMR Biogéosciences laboratory has been equipped with an X-ray microtomography device, the Skyscan 1174. This rather basic instrument is ideal for small, low-density samples, but has a fairly long acquisition time (around 45 minutes). The tube power is limited to 50 kV with a 1.3 megapixel detector, enabling 3D images to be generated with a minimum voxel size of 6 µm (under optimum conditions). Samples can be up to 50 mm long and 30 mm in diameter.

In 2018, the UMRt BioÉcoAgro team in Artois acquired a Bruker Skyscan 1275 microtomograph. This has a sealed tube with a focal diameter of 5 µm that can deliver a voltage ranging from 20 to 100 kV. It enables rapid acquisition of samples with a diameter of up to 96 mm and a maximum height of 120 mm. It can be used for a variety of applications.

Acquired in 2023 by the UMR Biogéosciences laboratory, this instrument offers improved features: higher spatial resolution, shorter acquisition times and the ability to scan larger samples than the Skyscan 1174. High-quality images can be acquired using a high-energy X-ray source (150 kV) and a sensitive, large-format 1920 × 1536 pixel planar sensor. This enables 3D

Skyscan 1275 from Bruker



Easytom S 150 - RX Solution

images to be generated with a minimum voxel size of 6 µm (under optimal conditions). Samples can measure up to 400 mm in length and 200 mm in diameter, and weigh up to 5 kg.

The instrument used to study the otoliths presented in this book is the Bruker Skyscan 1275 microtomograph from UMRt BioÉcoAgro.

For each species studied, three to five otoliths belonging to individuals of different sizes (and therefore ages) were scanned. The otoliths were placed on polystyrene supports and held in place with adhesive tape, which is radio-transparent (i.e. not visible on an X-ray). The supported otolith is then inserted into a plastic microtube, which is itself attached to the microtomograph's object holder (Figure 5).

The image acquisition parameters depend on the species. Otoliths vary in size and density. A 0.5 mm or 1 mm thick aluminium filter is required for image acquisition. The nominal resolution used is 10 µm for the vast majority of samples, but can reach 24 µm for the largest otoliths (appendix). Acquisition is performed over 360° with an angle step of 0.3°, generating 1,200 X-rays per otolith. Under these conditions, the acquisition time for each sample is around 40 minutes.

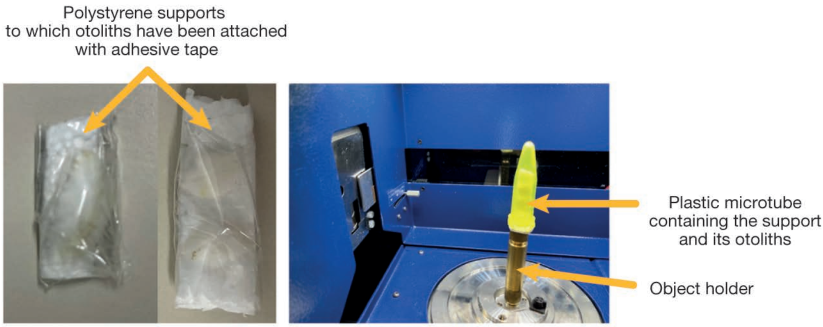


Figure 5. Preparation of otoliths for image acquisition using an X-ray microtomograph.

On the left, a photograph of otoliths fixed to a polystyrene support with adhesive tape; on the right, a photograph of the device used for image acquisition in the Skyscan 1275 microtomograph.

Image reconstruction

NRecon software (v.1.7.3.1) was used to reconstruct the cross-sections of the otoliths from the X-rays acquired by the microtomograph. The program uses Feldkamp's algorithm, a convolution and back-projection formula for reconstructing a three-dimensional density function from a set of two-dimensional projections. The X-rays acquired by microtomography are grey level equivalents of the densities of the materials (high densities are coded by high grey levels, i.e. tending towards white). The algorithm compiles this set of images into a volume of densities, then creates cross-sections of this volume at regular intervals. This reconstruction stage is automated and also enables parameters such as volume alignment, artefact correction and selection of areas of interest to be optimised. The slice images are saved in TIFF format.

Segmentation

The purpose of the virtual slice segmentation stage is to distinguish, in the 3D volume resulting from these slices, areas of interest corresponding to the objects under study. In this case, the voxels representing the otoliths are distinguished

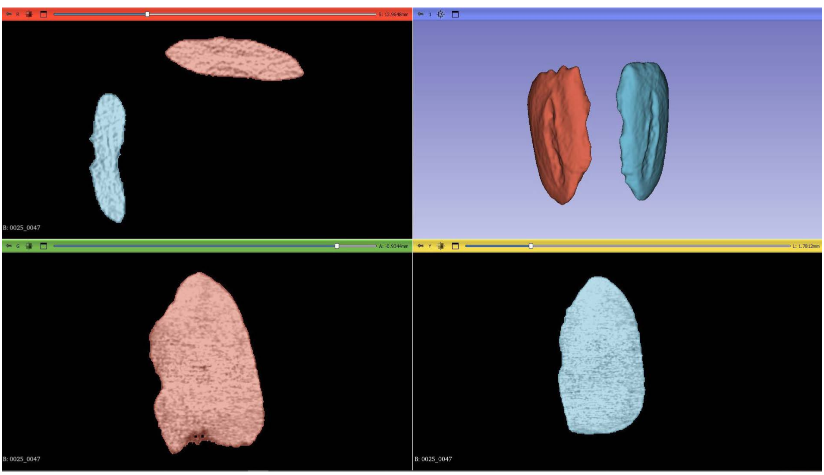


Figure 6. Opening otolith sections in 3D Slicer.

The sections are visualised in three orthogonal planes (in the three windows with black backgrounds). After segmentation of the otolith by thresholds, the 3D surface of the otolith is modelled in the form of a mesh (in the window with the blue background).

from the background voxels using simple grey level criteria (the otolith is dense relative to the background, so the voxels making it up will be light) and adjacency (the otolith is a continuous object). This segmentation stage is carried out using 3DSlicer software (v.4.10.2). A grey levels threshold is applied to select all the voxels making up the otoliths (Figure 6). The surface of this set of selected voxels is then extracted in the form of a 3D mesh. This type of object models a 3D surface in the form of a cloud of points (vertices) linked together by triangulation.

Extraction of otolith shape data

Spherical harmonics

The 3D surfaces of otoliths, modelled in the form of meshes derived from the segmentation of 3D volumes acquired by microtomography, are then analysed using geometric morphometry tools (see, for example, Claude, 2008, for an overview of the different tools). This discipline, used in the evolutionary sciences (biology and palaeontology), aims to quantify the morphological variations of organisms (as a whole or by focusing on certain parts) using mathematical means (geometry and statistics), and to understand the causes of these morphological variations (relationship with environmental factors, for example), their temporal evolution (from the developmental timescale to the palaeontological timescale) and their diversity (present or past).

Among the tools offered by geometric morphometry, we have used the spherical harmonics method (Spharm; Shen *et al.,* 2009) to characterise the 3D morphologies of otolith surfaces. This method is part of a broader approach to geometric morphometry known as contour analysis, which is mainly used in 2D and aims to describe the 2D contour using mathematical functions such as Fourier series (Claude, 2008). The contour is first discretised by a series of points, characterised by their x and y coordinates. The variations in these coordinates along the contour are then treated as signals by Fourier functions. These functions consist of a sum of sinusoidal terms (sine or cosine) of increasing frequency. The low-frequency terms describe the general aspects of the 2D contour (i.e. the 2D shape), and the high-frequency terms describe the finer details of this contour. The combination of these terms at different frequencies (through their sum) describes the 2D contour as a whole (both the general aspects and the local details). These sinusoidal terms are associated with coefficients that give greater or lesser weight to a particular term. Between different contours, it is these coefficients (weights) that reflect differences in appearance between 2D contours (and therefore differences in shape). For these coefficients to be comparable from one individual to another, a certain number of standardisations or normalisations are required prior to their calculation. For example, each contour is described by an identical number of regularly spaced points. The contours are also standardised in terms of their positions, sizes and orientations, which do not provide any information about differences in shape between individuals. In addition, the calculation of these Fourier series and coefficients remains sensitive to the direction of travel of the contours (clockwise or anti-clockwise) and the definition of a starting point on this path; these two aspects must also be standardised between individuals.

For 3D surfaces, the general principles of the Spharm method remain the same as for 2D contours:

– discretization of 3D surfaces using mesh vertices;

– approximation of these 3D surfaces by calculating spherical harmonics that describe the variations in x, y and z of these surfaces (Figure 7);

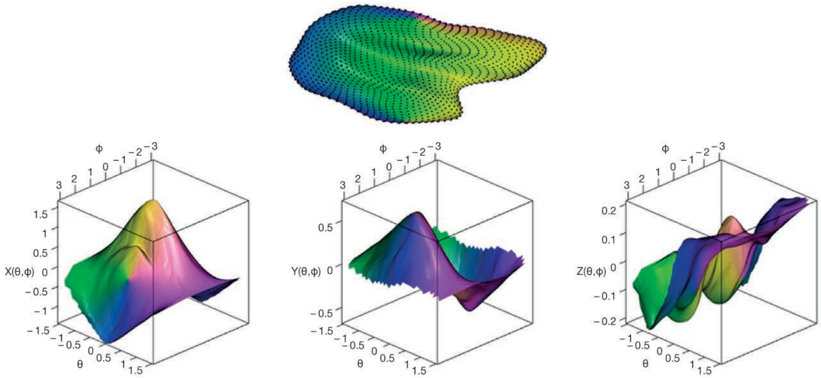


Figure 7. Representation of the three signals X(θ, Φ), Y(θ, Φ), and Z(θ, Φ) that will be processed by the Spharm analysis and decomposed into spherical harmonics.

The mesh of the pilchard otolith surface (top) is characterised by the Cartesian X, Y and Z coordinates of the vertexes (black dots) that make it up. Each of these vertices has a unique correspondence with each of the vertices in the reference sphere (Figure 9). The coordinates of the vertices of this sphere can be expressed as spherical coordinates (r, θ, Φ); a unique vertex of this sphere corresponds to each pair (θ, Φ) on the surface of the sphere, which can itself map uniquely onto the surface of the otolith. The three graphs in the bottom row thus represent the X, Y and Z variations of the vertices of the otolith mesh for each pair (θ, Φ) of the vertices of the reference sphere surface respectively. The colour gradient symbolises the homology of the vertices between the surfaces.

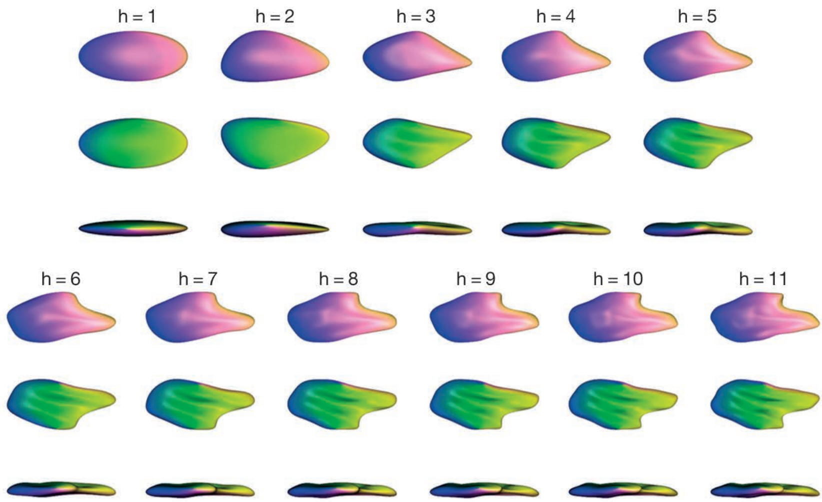


Figure 8. Visualisation of the effect of the number of harmonics (h) used to reconstruct the contour of a pilchard otolith.

This number varies per column, from one to 11 harmonics. Note that the greater the number of harmonics considered, the more accurately the otolith surface is reconstructed. However, above a certain number of harmonics (around nine here), the level of detail added by increasing this number becomes negligible. The colour gradient symbolises the vertex homology between the surfaces. Three orthogonal views of the otolith are displayed.

– calculation of coefficients derived from these spherical harmonic functions describing the rougher or finer details of surfaces according to the frequency of their harmonics (Figure 8).

The method will essentially differ in terms of the standardisations required prior to calculating these coefficients. Without going into the details, we can see, for example, that the binary choice of traversing a 2D contour clockwise or anti-clockwise no longer has any meaning for a 3D surface. So, to make the surfaces homologous to each other, the Spharm method involves mapping the vertices of the 3D surfaces onto a reference sphere, while identifying them as unique and homologous to each other (Figure 9). These steps correspond in 3D to the standardisation of contours (number of points and starting point) and their paths (clockwise or counter-clockwise) in 2D.

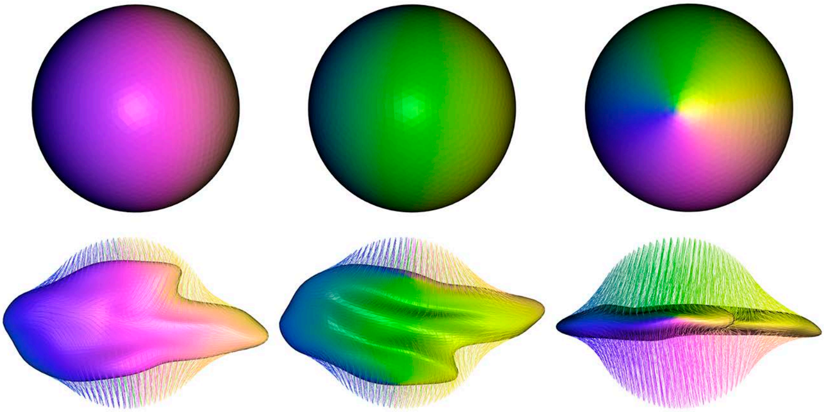


Figure 9. View of the surface mapping of a pilchard otolith (modelled as a mesh) on the reference sphere used in the Spharm analysis.

The colour gradient symbolises the vertex homology between the two surfaces. In the same way, the segments starting from the otolith mesh represent how the vertices of the sphere are projected onto the vertices of the otolith. Three orthogonal views are plotted. For a set of 3D surfaces, the Spharm method also estimates an average surface (reflecting an average otolith morphology). The individual surfaces are aligned with this average 3D surface, taken as a reference. For the subsequent analyses, the Spharm method was applied, using 11 harmonics and simplifying (by decimation) each individual mesh to 1,000 vertices. Prior to this process, six marker points (Figure 10) had to be placed on each mesh (to pre-orientate them), and the left otolith meshes were symmetrised to obtain straight shapes.

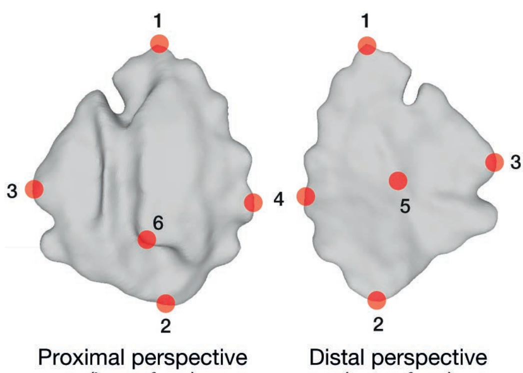


Figure 10. 3D volumes of the inner and outer otoliths with six marker points (red dots).

1: *rostrum*; 2: *postrostrum*; 3: dorsal extremity; 4: ventral extremity; 5: middle of outer surface of the otolith; 6: apex of *sulcus acusticus*.

Multivariate treatment

To summarise and visualise the main patterns of variation in otolith shape between species, the coefficients derived from the Spharm analysis for each individual were processed using principal component analysis (PCA). This multivariate statistical analysis is used to construct new, uncorrelated variables (called principal components or PCs) from the initial variables (in this case, the Spharm coefficients), each summarising a given aspect of the initial variance contained in the data. These components are ordered according to the amount of variance they explain (the first PC summarising more variance than the second, which explains more than the third, and so on). Starting with a series of initial variables that are partially correlated with each other (which is often the case in morphometry), it is expected that the initial variance contained in a large number of variables can be effectively summarised by just a few PCs. Bivariate graphs of PCs can thus be used to visualise the dispersion of individuals according to these PCs, and to visualise the morphological differences or similarities between these individuals. As each component summarises an aspect of morphological variation, we can also visualise this aspect of variation using theoretical 3D meshes (which do not directly reflect a real individual) calculated at the extremities of each of the PCs, which makes it possible to interpret the variations in shape explained by each PC, and hence the morphological differences or similarities between individuals.

These statistical analyses and the Spharm processing were carried out using R software (R Core Team, 2020, version 4.0.3).

Otolith size metrics

Based on the 3D meshes of the otoliths, a number of size metrics were estimated. To calculate the length, width and height of the otolith respectively, the distances between points 1 and 2, then 3 and 4, then 5 and 6 were calculated (Figure 10). In addition, the area and volume of the otolith were estimated with the functions vcgArea and vcgVolume from the Rvcg package of R (Schlager, 2017).

2. Species presentation

The order in which the species are presented was chosen so that those with the most similar otoliths are presented consecutively. This ranking was based on four criteria:

– morphotype: round fish, then flat fish;

– habitat, reflecting the position of the fish in the water column: pelagic species (evolving near the surface), demersal species (evolving in the central part of the water column) and then benthic species (evolving on the bottom and in close contact with it);

– taxonomy: species have been grouped according to the orders and families to which they belong;

– alphabetical order: lastly, alphabetical order was used for species with the same morphotype, habitat and taxonomic classification.

Each species is presented on a double-page spread.

The left-hand page presents the species: its biological characteristics, the environment in which it lives and the main features of its life cycle. All the information has been taken from the two summary reports coordinated by Ifremer (Mahé *et al.*, 2007; Carpentier *et al.*, 2009).

The right-hand page gives a detailed description of the otolith: its general description, the different views extracted from the 3D reconstruction of the left otolith of individuals distributed over the size range of the captures, the displayed length (total fish length measured from the tip of the head to that of the tail), the relationships between the otolith metrics (length, width, height, surface area and volume) and the total length of the fish, in addition to the evolution of the otolith over the life of the fish to enable identification of differences between life stages within the same species.

Atlantic herring

Latin name: *Clupea harengus*
Order: Clupeiformes
Family: Clupeidae
Morphotype: round fish

Distribution area

The Atlantic herring can be found in the waters of the North Atlantic continental shelf, from the White Sea and Iceland to the Strait of Gibraltar.

Environment

A pelagic fish, Atlantic herring live on the surface or in the water column at night, and congregate on the seabed during the day. Herring can be found from the surface to the bottom across the continental shelf (from 0 to 200 m depth). There is a positive correlation between bathymetry and fish size. The largest fish tend to be found in the deepest waters. Herring prefer gravelly and sandy sediments.

Biology and life cycle

Herring reach their first sexual maturity between the ages of four and five and at around 30 cm. They lay their eggs close to the seabed (5 to 20 m deep). In the Eastern Channel, the coastline from Fécamp to Dunkirk is a major herring spawning ground. The spawning season in the Eastern Channel starts at the end of November, peaks in December, declines in January and ends in February. The number of eggs laid is directly related to the size of the female. The eggs fall to the bottom and adhere to the substrate. From April onwards, the larvae can be found near the French coast between Boulogne-sur-Mer and Dieppe. The juveniles swim up into the North Sea before returning to the English Channel in autumn when they are ready to reproduce.

In the North Sea, there are three sub-populations that migrate to reproduce. The sub-population known as the Downs stock moves through the North Sea, but also through the Eastern Channel. Fish that spawn in the central North Sea, along the English coast and around the Dogger Bank, and those that spawn in the Downs stock share the same feeding grounds in the central North Sea, but separate to spawn each year. After spawning, the spawners migrate back to the central North Sea to feed during the summer. In autumn, the Downs herring spawners head back south, reappearing in the Channel in November.

Herring feed mainly on zooplankton (copepods, amphipods and mysids), following their daily vertical migrations. They choose their prey according to its size, but also according to the season.

Description of the otolith

Mostly oblong to elliptical in shape. Slightly lobed all around with age. The *rostrum* is prominent, as is the *antirostrum*, which represents a third of the size of the *rostrum*. The *ostium* is longer than the *cauda*, which is very shallow. Medium to small in size compared with other species of the same size.

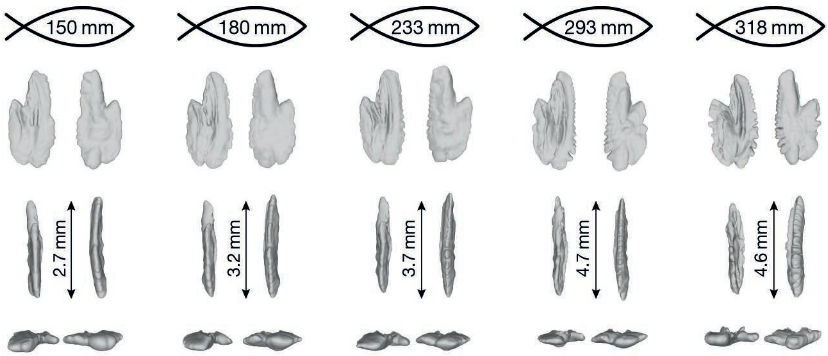


Figure 11. Changes in otolith shape and size over the lifetime of the Atlantic herring, represented by five individuals identified by their total length expressed in millimetres.

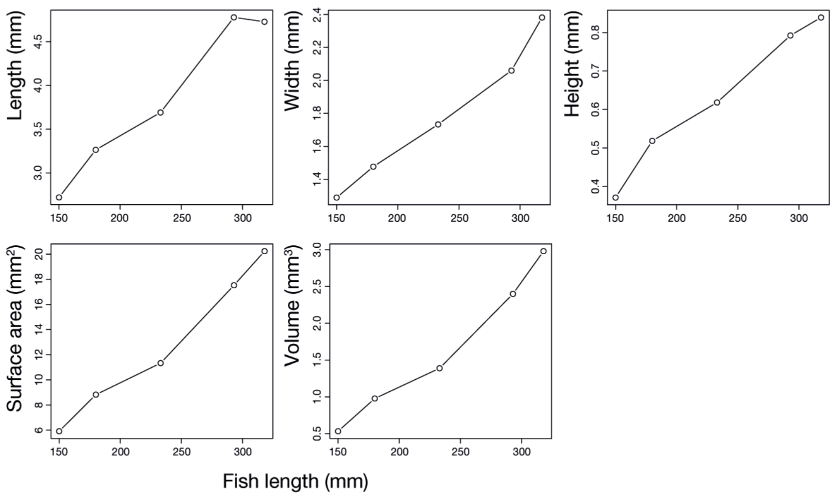


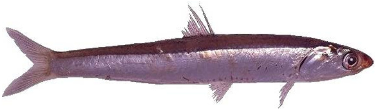
Figure 12. Relationships between otolith morphology and length in Atlantic herring.

Summary

The fish analysed measured between 15 and 32 cm, with otoliths between 2.7 and 4.6 mm long. This shows that otolith growth is relatively similar to that of the fish. However, the morphology of the herring otolith shows an evolving contour, becoming more and more serrated and therefore more complex with size. Similarly, the *sulcus* grows from anterior to posterior, particularly in the *cauda*.

European anchovy

Latin name: *Engraulis encrasicolus*
Order: Clupeiformes
Family: Engraulidae
Morphotype: round fish



Distribution area

The European anchovy is distributed in the North-East Atlantic from Morocco to the North and Baltic Seas and throughout the Mediterranean and Black Seas. It is particularly abundant along the Spanish coast and in the Bay of Biscay. In the 20th century, there was an anchovy fishery in the Wadden Sea, located to the east of the North Sea, which has completely disappeared since 1962. In recent years, however, anchovies have been present in the north-western North Sea and the English Channel.

Environment

A gregarious pelagic fish, the European anchovy lives in schools in the water column. It can be found from the coast to a depth of 150 m. Its way of life is linked more to the characteristics of the water masses than to particular depths or latitudes. In the north-western North Sea, the appearance of anchovy is directly linked to the rise in temperature, which allows the presence of "warm" zooplankton species, particularly calanoid copepods, in very northern areas. It can also be seen as far north as Scandinavia during some very warm years. Similarly, depending on the year, Celtic Sea anchovies may migrate to the English Channel. Finally, the abundance and growth of the anchovy are correlated with temperature and primary production.

Biology and life cycle

Anchovies reach their first sexual maturity at 11.5 cm in the Bay of Biscay, corresponding to an age of one year. Here, they reproduce from April to August; with the oldest fishes starting in April, followed by the youngest in May. Reproduction takes place during this period, as the high temperatures offer favourable feeding conditions.

It lays batches of around 30 eggs during the season, i.e. one every three to four days. Eggs are laid between 10pm and 2am, very close to the surface. The eggs and larvae then drift with the currents (passive migration). After spawning, from August to November, the anchovies grow rapidly (75% of annual growth).

Anchovies feed mainly on zooplankton, particularly on small crustaceans such as copepods, on mollusc larvae and on fish eggs and fry.

Description of the otolith

Elliptical and elongated. The *rostrum* is prominent and pointed, as is the *antirostrum*, although shorter and less pointed. The *rostrum* and *antirostrum* are convex on both sides. The *ostium* is longer than the *cauda* and is funnel-shaped. The *cauda* is linear and closed. The *sulcus* is strongly serrated.

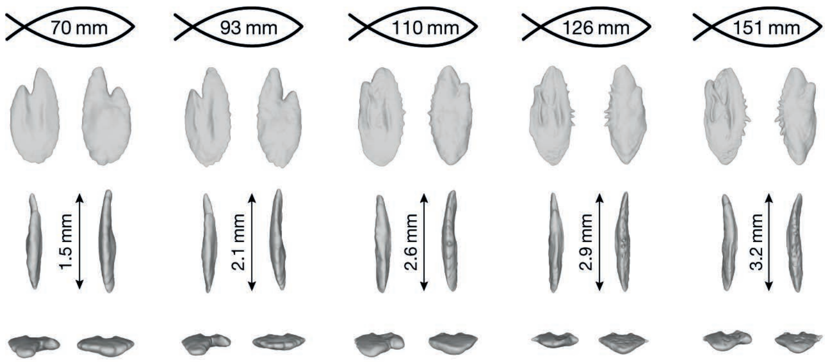


Figure 13. Changes in otolith shape and size during the life of the European anchovy, represented by five individuals identified by their total length expressed in millimetres.

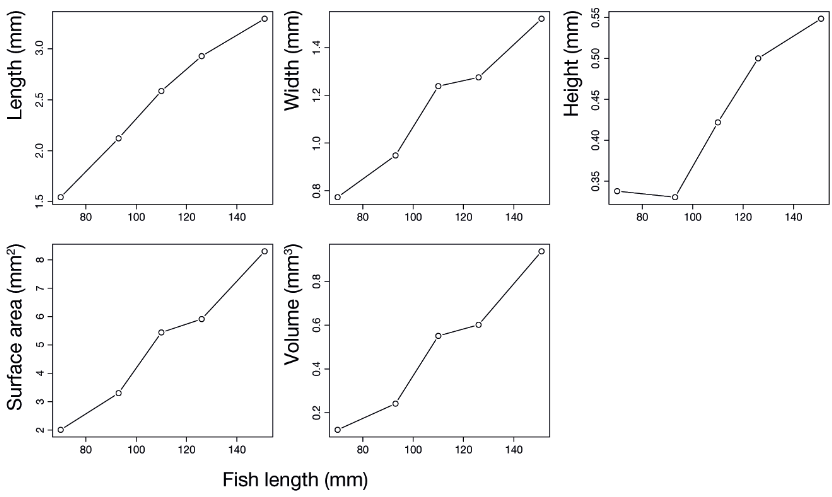


Figure 14. Relationships between otolith morphology and length in European anchovy.

Summary

The fish analysed measured between 7 and 16 cm for otoliths with lengths of between 1.5 and 3.2 mm. This shows that otoliths grow at a rate comparable to that of the fish. Anchovy otoliths show a rapid increase in length and width. Conversely, the height of the otolith increases as soon as the fish exceeds 10 cm. Note that the shape changes, with otoliths showing a very marked *excisura* for fish between 7 and 10 cm. This zone is then much less marked in adults, but the external shape becomes more serrated.

European pilchard

Latin name: *Sardina pilchardus*
Order: Clupeiformes
Family: Clupeidae
Morphotype: round fish

Distribution area

The European pilchard lives in the North-East Atlantic, from Norway and Scotland to Senegal. The northern Atlantic pilchard is fished as far north as the Irish waters and south of the North Sea, although the two main fishing grounds are the Bay of Biscay and the English Channel. It is also found and fished in the Mediterranean.

Environment

A gregarious pelagic fish, the pilchard lives in shoals that can be very large, located near the surface at night (15 to 40 m depth) and deeper during the day (30 to 50 m depth), from coastal waters to 120 m deep. The distribution of pilchard is strongly influenced by temperature. In the north-west of the North Sea, the appearance of pilchard is directly linked to the increase in temperature, which allows the presence of "warm" zooplankton species, particularly calanoid copepods, in very northern areas. In addition, the northern Atlantic pilchard is divided into two groups that differ in their phenotype, which is directly linked to environmental conditions (temperature and salinity) during their larval development.

Biology and life cycle

Pilchards reach their first sexual maturity at around 19 cm in the English Channel. Growth is similar between males and females. Pilchards reproduce during upwelling, which affects temperature and productivity, and therefore the availability of prey. Reproduction occurs when the temperature is between 10 and 16 °C.

In the English Channel, the spawning area changes from west to east from March to August, followed by a westward return of pilchard from September to November. This results in two peaks in egg abundance in the eastern Channel from May to June, then from October to November. The eggs, then the larvae, are transported by currents, but also by upwelling.

In the North Atlantic Ocean, two sub-populations have been identified: the Iberian pilchard (also known as the Atlantic pilchard), from Gibraltar to the north coast of Spain, and the northern Atlantic pilchard, from the south of the Bay of Biscay to the northern limit of its distribution.

Description of the otolith

Mostly elliptical in shape. Lobed on the ventral margin. The *rostrum* is prominent, as is the *antirostrum*, but the latter is much shorter. The *ostium* is longer than the *cauda*, which is very shallow. The ventral margin is fairly straight. Medium to small in size compared to other species of the same size.

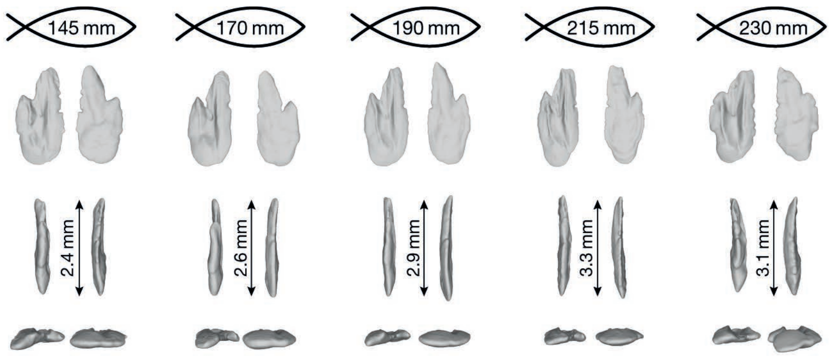


Figure 15. Changes in otolith shape and size over the lifetime of the European pilchard, represented by five individuals identified by their total length expressed in millimetres.

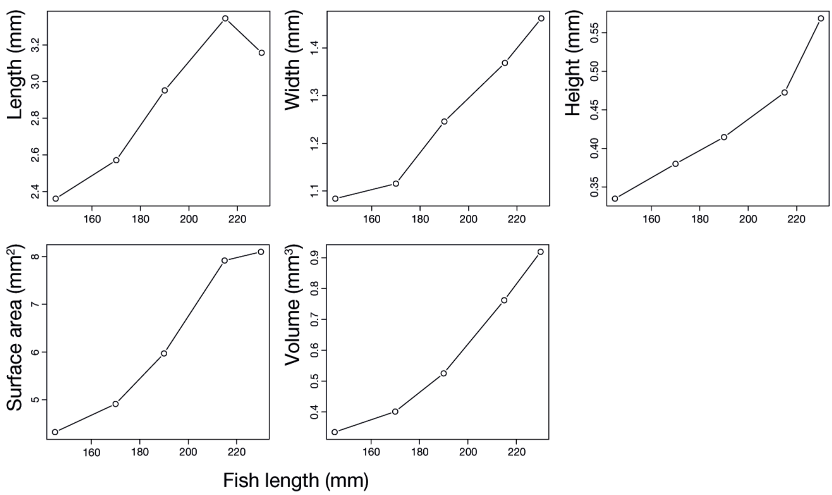


Figure 16. Relationships between otolith morphology and length in European pilchard.

Summary

The fish analysed measured between 14 and 23 cm, with otoliths between 2.4 and 3.1 mm long. This shows that otolith growth is relatively similar to that of the fish. Furthermore, the morphology of the otolith does not change greatly during the life of the pilchard.

Sprat

Latin name: *Sprattus sprattus*
Order: Clupeiformes
Family: Clupeidae
Morphotype: round fish

Distribution area

The sprat is found in the North-East Atlantic, from the Lofoten Islands to the Bay of Biscay, the English Channel, the North Sea, the Baltic Sea, the northern Mediterranean and the Black Sea.

Environment

A coastal pelagic fish (from the surface to a depth of 50 m), sometimes living very close to the coast and entering estuaries (largely the young individuals). Sprat stay close to the bottom during the day and rise to the surface at night.

Biology and life cycle

Sprat form very large concentrations and migrate widely between feeding grounds in winter and spawning grounds in spring and summer.

It reaches its first sexual maturity between 8 and 10 cm in the North Sea. Breeding takes place from January onwards in the English Channel. Still in the Channel, the larvae are widely distributed throughout the area, with the exception of the Capes of the Pas-de-Calais and the southern coasts of Normandy.

Sprat fry feed on diatoms and copepod eggs and larvae. Adults eat zooplankton, mainly planktonic crustaceans (copepods).

Description of the otolith

Oval in shape. Irregular on the ventral margin. Shorter and rounder than those of other clupeids. The *rostrum* is prominent. The *antirostrum* is also fairly well developed, but rounded. The *sulcus* is fairly deep with an *ostium* longer than the *cauda*. Medium to small in size compared to other species of the same size.

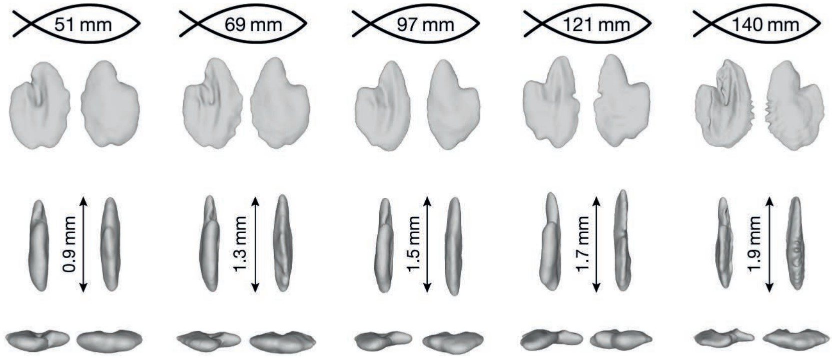


Figure 17. Changes in otolith shape and size over the life of the sprat, represented by five individuals identified by their total length expressed in millimetres.

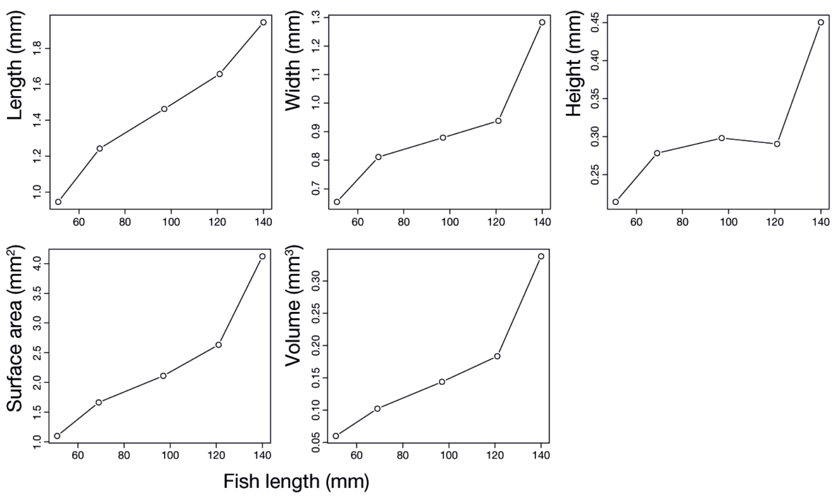


Figure 18. Relationships between otolith morphology and length in sprat.

Summary

The fish analysed measured between 5 and 14 cm, with otoliths between 0.9 and 1.9 mm long. This shows that otoliths grow more slowly than the fish. The mostly rounded edges may become serrated in larger individuals. As the sprat grows, the area between the *rostrum* and the *antirostrum* with the *excisura* deepens.

Atlantic horse mackerel

Latin name: *Trachurus trachurus*
Order: Carangiformes
Family: Carangidae
Morphotype: round fish

Distribution area

Atlantic horse mackerel can be found in the waters of the North-East Atlantic continental shelf, from Iceland to the Cape Verde Islands. This fish is considered an abundant species in the Eastern Channel and the North Sea. It is also found in the Mediterranean and Marmara Seas, and more rarely in the Black Sea.

Environment

A highly migratory pelagic fish and, the Atlantic horse mackerel lives in the water column or near the bottom. It is found on the continental slope and generally at depths of less than 200 m.

Biology and life cycle

Atlantic horse mackerel reproduce along the continental shelf, off the west coast of Ireland, in the Celtic Sea, in the Bay of Biscay and close to the Iberian Peninsula from the age of three for the male (20-22 cm) and from the age of four or five for the female (26-30 cm). They breed in the eastern English Channel and the southern North Sea from late May to August, while the breeding season in the Bay of Biscay runs from March to July north of the 46th parallel, and from January to August in the south.

After spawning in southern waters, Atlantic horse mackerel migrate northwards along the continental slope during June and July. They then migrate through the English Channel and into the North Sea along the Dutch and Danish coasts, where they lay their eggs in July and August. They remain off the Norwegian coast until September. From October to the end of November, they migrate southwards via the North Sea and then the English Channel.

At the end of their first year of life, the Atlantic horse mackerel, reaching a size of around 10 cm, gather in the upper part of the water column and form shoals away from larger fish.

Description of the otolith

Lanceolate, with a prominent pointed *rostrum* and a small *antirostrum*. Dorsal margin smooth and fairly linear, and ventral margin irregular and convex. The *sulcus* is present from the anterior margin to near the posterior margin. The *cauda* is twice as long as the *ostium*, and curved towards the shallow ventral margin. Quite large compared to other species of the same size.

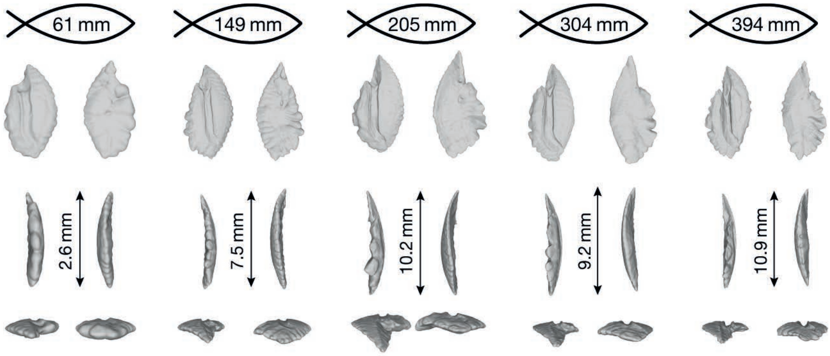


Figure 19. Changes in otolith shape and size over the lifetime of the Atlantic horse mackerel, represented by five individuals identified by their total length expressed in millimetres.

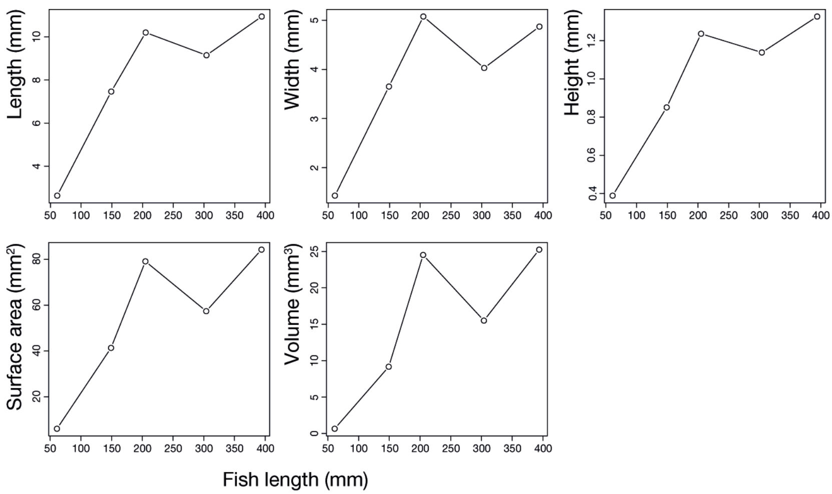


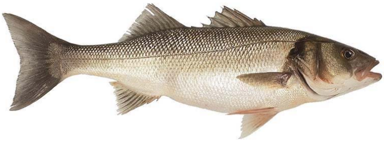
Figure 20. Relationships between otolith morphology and length in Atlantic horse mackerel.

Summary

The fish analysed measured between 6 and 40 cm, with otoliths ranging in length from 2.6 to 10.9 mm. This shows that otoliths grow faster than fish. The Atlantic horse mackerel otolith shows a rapid increase in all morphological parameters for the size range 6 to 20 cm, after which the its size does not vary greatly. While the size of the otolith changes with ontogeny, its morphology fluctuates little when comparing the five fish, despite their very different sizes.

European seabass

Latin name: *Dicentrarchus labrax*
Order: Eupercaria
Family: Moronidae
Morphotype: round fish



Distribution area

European seabass can be found in the North-East Atlantic, from 30° North (coast of Morocco) to 60° North (southern Norway). It can be found in the Irish, North and Baltic Seas, and has colonised the whole of the Mediterranean and Black Seas.

Environment

A coastal bentho-demersal fish, particularly common along rocky coasts. It is a euryhaline fish, as it is able to withstand wide variations in salinity: from 0.5 ppm to over 40 ppm.

Biology and life cycle

European seabass reach their first sexual maturity between 35 and 40 cm. They reproduce in the western Channel at the start of the breeding season (mid-February), gradually moving eastwards until the end of June. The pelagic eggs take two to five days to hatch in the Channel. Once they arrive in the coastal zone, the larvae spend around 30 days there, the time necessary to reach the development stage corresponding to a size of 10 mm. This size enables them to enter estuarine areas for further development.

In the Channel and around the British Isles, juveniles remain in their estuary for at least the first three years of their lives. Seabass subsequently begin to migrate from the age of four. Larvae and juveniles live in shallow waters, generally less than 5 m deep, while adults are found in deeper, although still coastal, waters. Fry and juveniles have been observed in bays and estuaries in the English Channel and in the Bay of Biscay.

Adult seabass leave their summer feeding grounds in September-October and head for wintering grounds further south (mainly in the western Channel), where the waters remain warmer. From February onwards, they begin their ascent northwards or north-eastwards, towards the summer feeding grounds, which they reach around May-June. The major movements that can be described as annual migrations therefore take place in autumn-winter. In contrast, summer movements appear to be much more limited and confined to coastal areas. This annual migration pattern is accepted for seabass around the British Isles.

Seabass are voracious carnivorous predators that can consume large prey. They hunt both day and night, on the seabed or in the water column. They are also capable of herbivory.

Description of the otolith

Oval to oblong in shape. Slightly lobed on the dorsal margin, which is fairly linear. The ventral margin is shallowly V-shaped. The *rostrum* is prominent and long, with a short *antirostrum*, but also quite developed. Proximal side very convex and distal side very concave. *Cauda* fairly deep, curved. Quite large compared to other species of the same size.

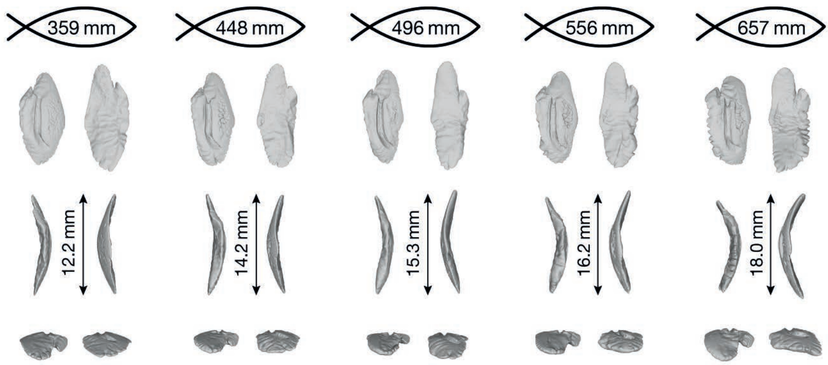


Figure 21. Changes in otolith shape and size over the lifetime of the European seabass, represented by five individuals identified by their total length expressed in millimetres.

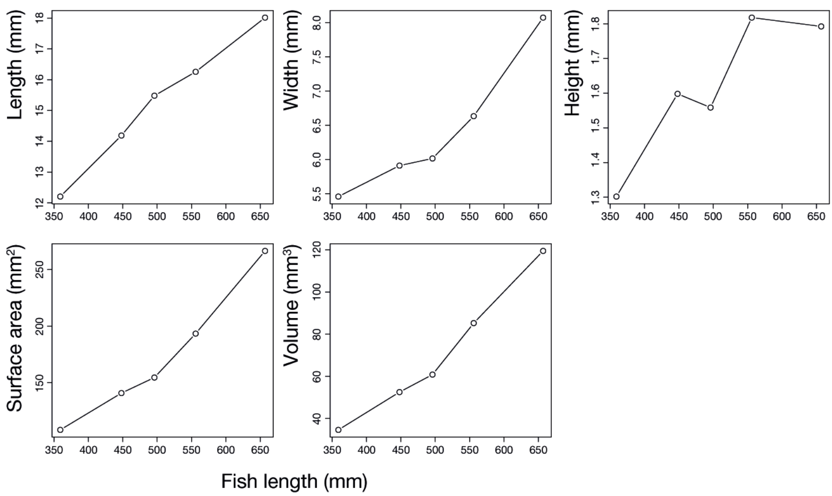


Figure 22. Relationships between otolith morphology and length in European seabass.

Summary

The fish analysed measured between 35 and 66 cm, with otoliths between 12.2 and 18 mm long. This shows that the otolith grows more slowly than the fish. For seabass over 50 cm long, the otoliths are taller, mainly due to the proximal surface, which becomes increasingly convex.

John Dory

Latin name: *Zeus faber*
Order: Zeiformes
Family: Zeidae
Morphotype: round fish

Distribution area

The John Dory appears to be a species with a wide distribution. It can be found in the Eastern Atlantic, from South Africa to the Faroe Islands and Norway, in the Mediterranean, the Black Sea, the Indian Ocean, New Zealand, Japan and Korea.

Environment

A demersal fish that mainly inhabits soft, muddy bottoms. It lives on the shelf and continental slope to a depth of 600 m. Beyond a depth of 100 m, only large individuals (>30 cm) are present during the winter. Maximum abundances of this fish have been observed at depths of between 50 and 120 m.

Biology and life cycle

The John Dory begins to reproduce as soon as it reaches a size of between 30 and 35 cm. Breeding takes place between June and August in the Bay of Biscay, and the Celtic, Irish, and Mediterranean Seas, while it does not occur until late winter in Mauritania. The eggs are pelagic. The nursery areas are unknown in the Channel and North Sea. Juveniles have, however, been observed in the Channel, on the west coast of Scotland and in the North Sea. These observations show that the juveniles are mainly distributed near the coast.

The John Dory mostly feeds on small fish, but also on cephalopods and crustaceans.

Description of the otolith

Three-lobed, with anterior and posterior constrictions revealing three lobes in three different directions, and a small collicular ridge at the *sulcus* between the *cauda* and the *ostium*. This shape cannot be confused with the otolith of another species. Smooth margins.

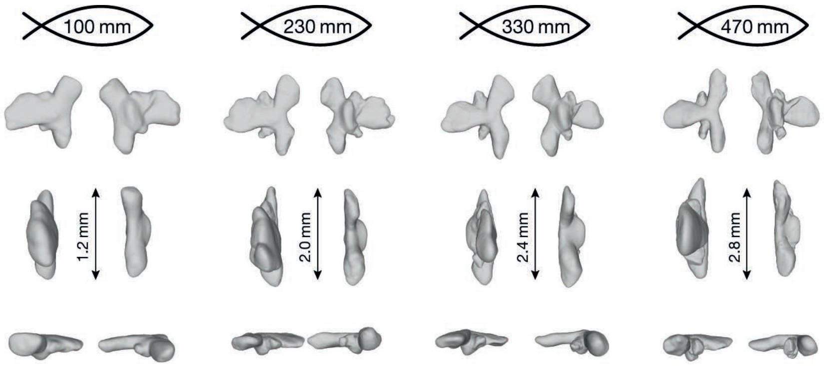


Figure 23. Changes in otolith shape and size over the lifetime of the John Dory, represented by four individuals identified by their total length expressed in millimetres.

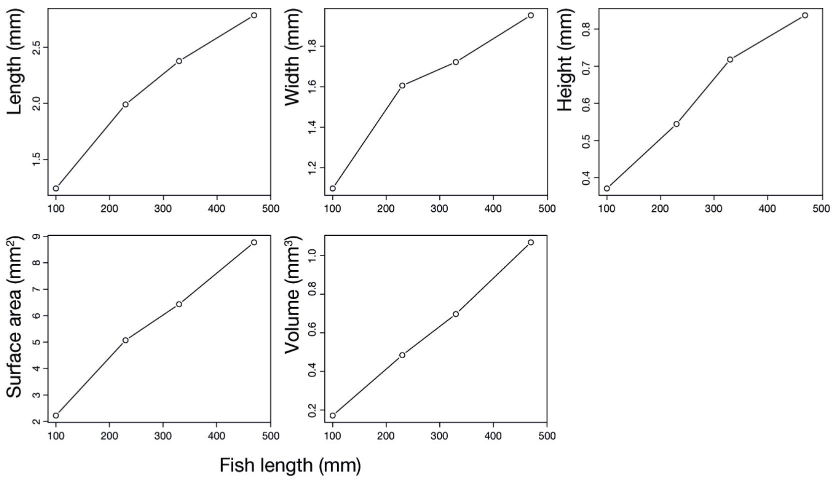


Figure 24. Relationships between otolith morphology and length in John Dory.

Summary

The fish analysed measured between 10 and 47 cm, with otoliths between 1.2 and 2.8 mm long. This shows that the otoliths grow more slowly than the fish. The characteristic shape of the otolith does not change throughout the life of the John Dory, only its size increases. The otolith is trilobate in three different growth directions, with relatively proportional growth in length, width and height throughout the life of the fish.

Atlantic mackerel

Latin name: *Scomber scombrus*
Order: Scombriformes
Family: Scombridae
Morphotype: round fish

Distribution area

Atlantic mackerel can be found in the waters of the continental shelf of the North-East Atlantic, generally from Iceland and the Norwegian coast in the north to the coast of Africa in the south. It also lives in the Mediterranean and Black Seas. Finally, it can also be found off the coast of North America in the North-West Atlantic.

Environment

A pelagic fish that lives in areas from 0 to 250 m depth, but is mainly present in the water column between the surface and 40 m.

Biology and life cycle

On average, Atlantic mackerel reach their first sexual maturity in the Bay of Biscay when they are two years old, which can be generalized to the North-East Atlantic. They breed from the south, around the coasts to the north-west of Spain, to the north, along the Norwegian coast. The breeding season runs from March to July. Spawning occurs earlier in the south than in the north, as it depends on the surface temperature, which must be between 13 and 15.5 °C. The juveniles grow in coastal areas, where they remain until they begin their autumn migration to the wintering grounds, except in the coastal waters of Cornwall, where they remain for their first few winters.

Atlantic mackerel are highly migratory and feed mainly on zooplankton. They are excellent swimmers, with speeds of up to $6 m.s^{-1}$. They are gregarious by nature, and mackerel shoals can vary in size from one to seven tonnes. Mackerel migrations are directly linked to those of copepods, which partly explains their vertical migrations during the day. There are two main populations in the North-East Atlantic: the North Sea population, which winters in the Norwegian Trench, and the Celtic Sea population, which winters in the south-east of England around Cornwall, in the west of the western English Channel, and around the north of Scotland. At the end of winter in February-March, the North Sea population migrates mainly towards the centre of the North Sea and the Skagerrak to reproduce, while the Celtic Sea population come together to breed along the 200 m isobath between southern Ireland and western Brittany.

Description of the otolith

Lanceolate, with a very prominent *rostrum* and blunt *antirostrum*. Ventral margin fairly linear, and dorsal margin irregular and convex. The *sulcus* is present along its entire length. The *cauda* is deep, wide, curved towards the ventral margin and open. The *ostium* is very wide and open. Medium-sized compared to other species of the same size.

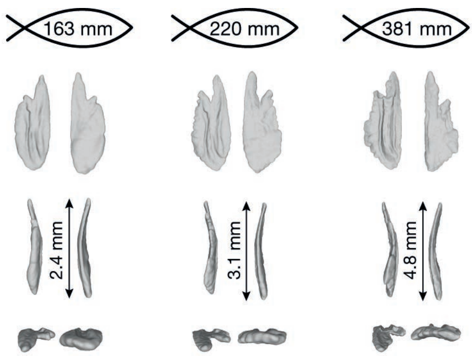


Figure 25. Changes in otolith shape and size over the lifetime of the Atlantic mackerel, represented by three individuals identified by their total length expressed in millimetres.

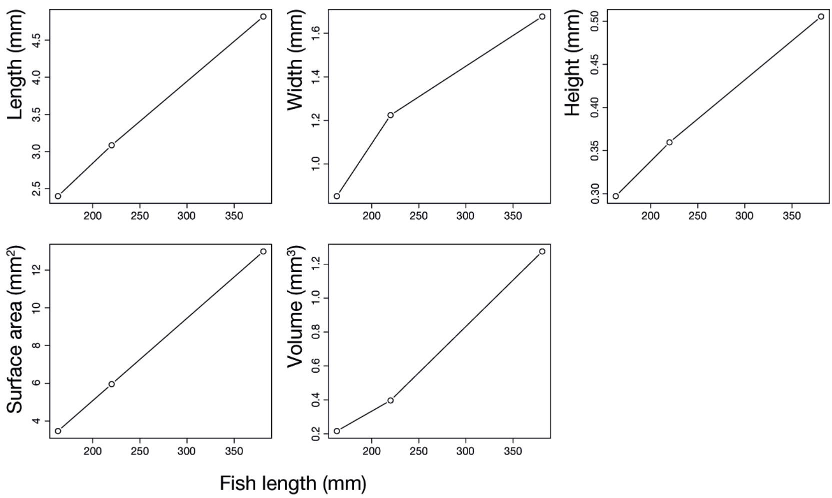


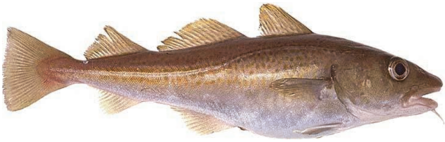
Figure 26. Relationships between otolith morphology and length in Atlantic mackerel.

Summary

The fish analysed measured between 16 and 39 cm, with otoliths ranging in length from 2.4 to 4.8 mm. This shows that the otoliths grow at a relatively similar rate to the fish. The otolith changes in three respects over the course of a mackerel's life: the largely rounded edges may become serrated in larger individuals, the area between the *rostrum* and the *antirostrum* with the *excisura* becomes increasingly pronounced, and the *sulcus* deepens and widens.

Atlantic cod

Latin name: *Gadus morhua*
Order: Gadiformes
Family: Gadidae
Morphotype: round fish



Distribution area

Atlantic cod is found in the North Atlantic. In the west, it ranges from Iceland to the east and west coasts of Greenland and the coasts of Canada, and as far south as Cape Hatteras in North Carolina. In the east, its range extends from Brittany and the Celtic Sea in the south northward to the Barents and Baltic Seas.

Environment

A bentho-demersal fish that lives in schools only during the day, but can also be found in open water between 0 and 600 m, with high abundance between 150 and 200 m. This boreal species is found in marine to brackish waters with temperatures between 0 and 20 °C. In the North Sea, it is caught in waters ranging from 20 m in the northern part to 200 m in the north-west. These waters have temperatures around 6 °C and a salinity of 29 to 35‰. In the eastern Channel, it is fished mainly in the Pas-de-Calais Strait, and in the Bay of Seine. These waters have a temperature of around 17 °C and a salinity between 33 to 35‰. The juveniles were observed mainly near the coast on bottoms made up of fine sediments.

Biology and life cycle

Atlantic cod reach their first sexual maturity in the Channel around 59 cm for females and 53 cm for males (Dorel, 1986). While 23% of three-year-old individuals are sexually mature, this percentage rises to 62% for four-year-old fish (ICES, 2006). In the eastern Channel and southern North Sea, the spawning period extends from January to April, with a peak at the end of February (Van der Land *et al.,* 1990). The pelagic eggs hatch after around 12 days into larvae that remain pelagic for two to five months before migrating to the bottom. The fry grow rapidly. Spawning grounds are known in the eastern Channel, mainly in the coastal waters of southern England, off Dieppe, and in the Bay of Seine (Bennet *et al.*, 1993; ICES, 2002).

As an adult, the Atlantic cod is an active predator, feeding on invertebrates (decapod crustaceans, cephalopods, worms) and small fish around dawn or dusk. Cod form shoals during the day, which break up at night. Most populations have separate spawning and feeding grounds, involving seasonal migrations.

Description of the otolith

Elliptical shape, with an oblong *rostrum* and a pointed posterior part. No *anti-rostrum*. The otolith is proximally concave and distally convex, and is lobed along its entire contour. The linear *sulcus* covers more than 90% of the proximal surface. Large compared to other species of the same size.

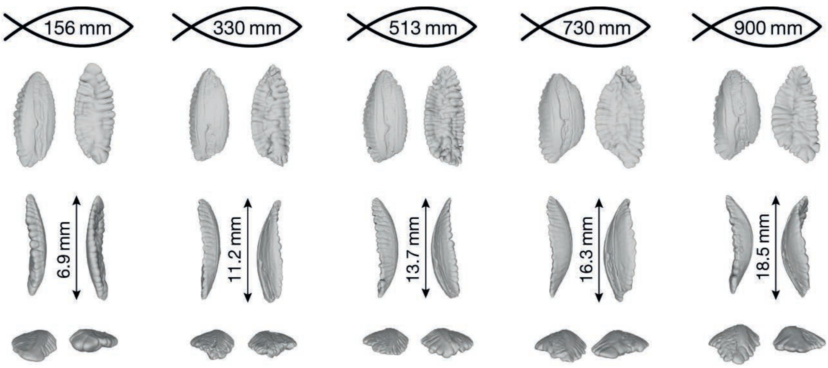


Figure 27. Changes in otolith shape and size over the lifetime of the Atlantic cod, represented by five individuals identified by their total length expressed in millimetres.

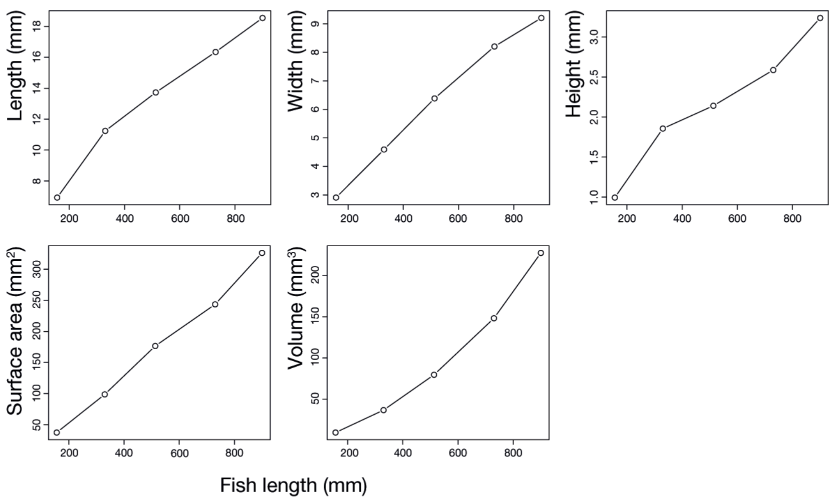


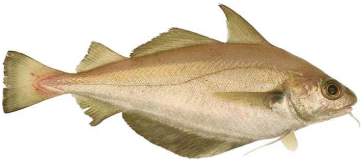
Figure 28. Relationships between otolith morphology and length in Atlantic cod.

Summary

The fish analysed measured between 15 and 90 cm, with otoliths ranging in length from 6.9 to 18.5 mm. This shows that otoliths grow more slowly than the fish. The morphology of the otolith does not change much over the lifetime of the cod, with only the lobes on the distal external surface appearing to be more pronounced in larger fish.

Pouting

Latin name: *Trisopterus luscus*
Order: Gadiformes
Family: Gadidae
Morphotype: round fish



Distribution area

The pouting is a species found in the North-East Atlantic, from southern Norway to Morocco, and in the north-western Mediterranean, from Spain to Greece, including the Adriatic Sea. The pouting is particularly abundant in the English Channel, the southern North Sea, and the Bay of Biscay.

Environment

A demersal fish, it prefers shallow waters, from the surface near the coast to depths of 100 to 150 m, rarely deeper. In the Bay of Biscay, it is found on the sandy bottom of the continental shelf, but high abundances coincide with the presence of rocks or wrecks around which this species congregates.

Biology and life cycle

The pouting breeds from the age of one year (20 to 25 cm) on bottoms deeper than 50 m in the central part of the Channel. The breeding season runs from January to April in the northern Bay of Biscay, from February to June in the eastern Channel, and from March to July in the North Sea. Pelagic eggs incubate for 10 to 12 days before becoming larvae, which migrate to the bottom. The juveniles live close to the coast. In the eastern Channel, the Bay of Seine has been identified as a nursery for this species. The pouting can enter estuaries and semi-enclosed lagoons, depending on temperature and salinity. As adults, they live in shoals and the only known movements are out to sea to breed and then back to the coast during the non-breeding phase.

During its first year of life, the pouting feeds mainly on crustaceans such as prawns and green crabs. Adult pouting continue to feed on crustaceans, but also on fish, cephalopod molluscs and annelid polychaetes.

Description of the otolith

Spindle-shaped, with a very short, blunt *rostrum*, an oblique anterior margin and a very pointed posterior margin. No *antirostrum*. Lobed on ventral margin and distal surface. The *sulcus* is present from the anterior margin to the posterior margin, fairly linear and closed at both ends. Large compared to other species of the same size.

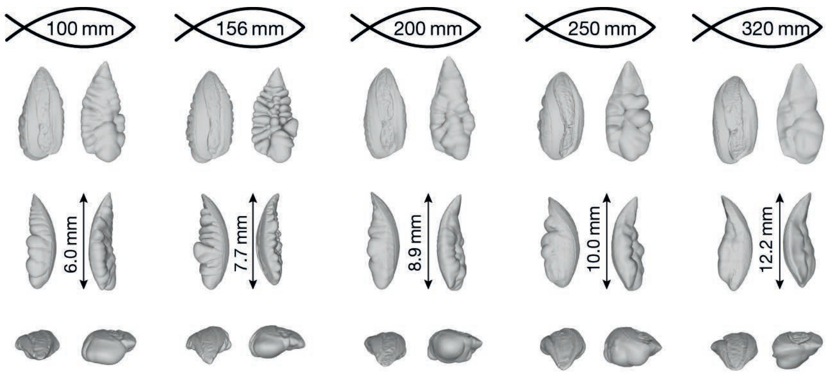


Figure 29. Changes in otolith shape and size during the life of the pouting, represented by five individuals identified by their total length expressed in millimetres.

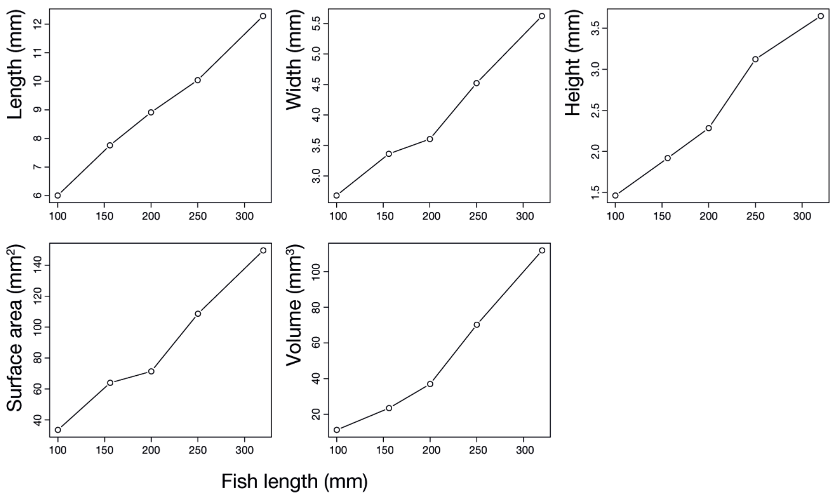


Figure 30. Relationships between otolith morphology and length in pouting.

Summary

The fish analysed measured between 10 and 32 cm, with otoliths between 6 and 12.2 mm long. This shows that the otolith grows more slowly than the fish. The shape of the otolith does not change much during the life of the pouting, with a relatively pointed *rostrum*, a particularly large height for an otolith of this size, and a distal external surface with largely numerous and prominent lobes.

Whiting

Latin name: *Merlangius merlangus*
Order: Gadiformes
Family: Gadidae
Morphotype: round fish

Distribution area

Whiting is found in the waters of the North-East Atlantic, from the north of Norway and Iceland to Ireland, where it is rarer. They are abundant in the North and Irish Seas and the English Channel. In the Eastern Channel-North Sea area, whiting move more towards the Eastern Channel and the southern North Sea from January to March, returning to the southern part of the central North Sea between June and October.

Environment

A bentho-demersal fish, meaning it lives close to the bottom. It is found on gravelly or muddy seabeds between 10 and 200 m, with a maximum between 30 and 100 m.

Biology and life cycle

Whiting begin to reproduce when they are around two years old, corresponding to a size of 20 to 30 cm. In the eastern Channel, the breeding season begins in December-January, intensifies in February and ends around June. Spawning grounds have been identified in the central English Channel and at depths of 40 to 80 m in the Bay of Biscay. After incubating for around 10 days, the eggs and then the larvae form the pelagic phase of the whiting's life. The larvae migrate towards the coast. The nurseries in the Channel are well identified, both near the coast and in estuaries such as the Bristol Channel and French estuaries.

The whiting's diet consists mainly of fish and crustaceans. Crustaceans are the preferred prey of juveniles. In adulthood, fish make up the bulk of the whiting's diet. Studies have revealed no evidence of cannibalism in whiting.

Description of the otolith

Elongated and narrow, reminiscent of a spindle, with a rounded, oblong *rostrum* and a very pointed posterior part. No *antirostrum*. Lobed over the entire contour, except for the posterior caudal part which is smoother, regardless of size. Large compared to other species of the same size.

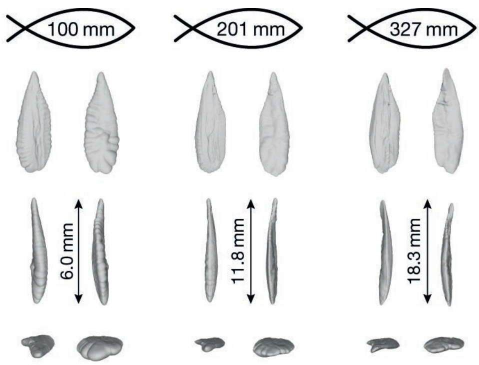


Figure 31. Changes in otolith shape and size over the lifetime of the whiting, represented by three individuals identified by their total length expressed in millimetres.

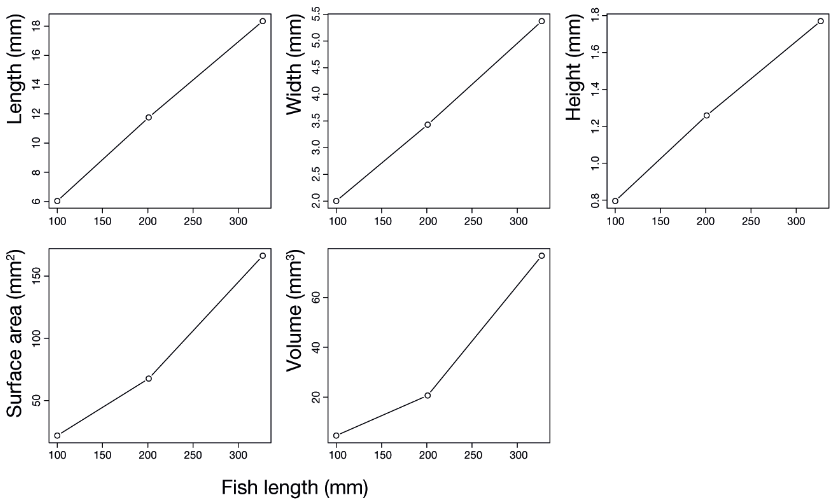


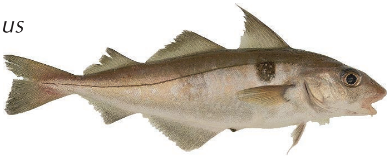
Figure 32. Relationships between otolith morphology and length in whiting.

Summary

The fish analysed measured between 10 and 33 cm, with otoliths ranging in length from 6 to 18.3 mm. This shows that the otolith grows in a similar way to the fish. The morphology of the otolith changes slightly with age, with the lobes on the distal outer surface diminishing over the life of the whiting.

Haddock

Latin name: *Melanogrammus aeglefinus*
Order: Gadiformes
Family: Gadidae
Morphotype: round fish



Distribution area

Haddock can be found in the North-East Atlantic, from Portugal to Svalbard (Arctic Ocean), as well as in the Barents Sea and around Iceland. In the North Sea, it is mainly found north of the Dogger Bank.

Environment

A bentho-demersal fish generally living at depths of between 10 and 400 m, and sometimes in the water column. Adults are more commonly found between 80 and 200 m, on rocks, sand, gravel or shells and in water temperatures between four and 10 °C.

Biology and life cycle

Haddock reproduce as soon as they reach sexual maturity, between 30 and 35 cm. They reproduce intermittently between January and July. They lay their eggs at a depth of 100-150 m from February to July in the northern North Sea, with a peak in spawning in late March or early April.

Haddock live in schools and migrate to feed and reproduce. They can undertake long migrations. They feed mainly on small, bottom-dwelling organisms, including crustaceans, molluscs, echinoderms, worms and fish (sand eels, capelin, herring, etc.).

Description of the otolith

Oval-shaped, with an oblique *rostrum* and a pointed posterior part. No *anti-rostrum*. Slightly lobed all around, strongly convex proximally. The dorsal margin is linear. The *sulcus* covers more than 90% of the proximal surface. Large compared to other species of the same size.

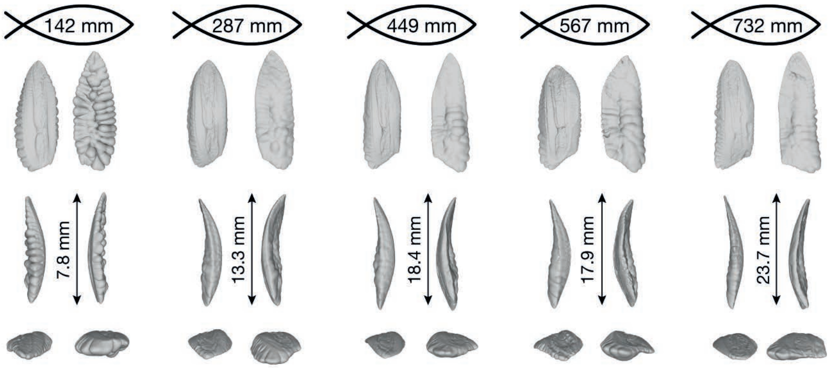


Figure 33. Changes in otolith shape and size over the lifetime of the haddock, represented by five individuals identified by their total length expressed in millimetres.

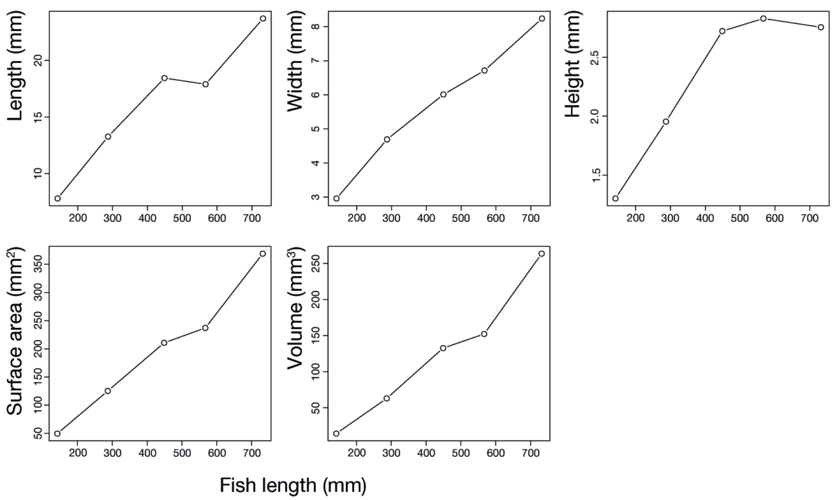


Figure 34. Relationships between otolith morphology and length in haddock.

Summary

The fish analysed measured between 14 and 74 cm, with otoliths ranging in length from 7.8 to 23.7 mm. This shows that the otolith grows more slowly than the fish. The morphology of the otolith changes over the lifetime of the haddock, however, with the lobes on the distal outer surface diminishing and, most notably, the thickness of the otolith increasing sharply for fish over 40 cm.

Red gurnard

Latin name: *Chelidonichthys cuculus*
Order: Perciformes
Family: Triglidae
Morphotype: round fish

Distribution area

The red gurnard is found in the North-East Atlantic, from southern Norway and the northern British Isles to Mauritania. It can also be found in the Mediterranean Sea and along the coasts of West Africa south to the latitude of Cape Verde in Senegal.

Environment

A benthic fish living on bottoms between 0 and 200 m deep, it is mainly found on bottoms made up of coarse sand and gravel on the continental shelf at depths of 30 to 60 m in the eastern Channel, and around 130 m in the Bay of Biscay.

Biology and life cycle

The red gurnard first reproduces between 25 and 28 cm, which corresponds to individuals aged one or two years. Spawning begins in February and it seems that the fish move westwards after spawning. Spawning is completed between June and August, the period during which the majority of fish are caught in the western Channel. Variations in the sex ratio of commercial catches suggest that the females return to the central Channel before the males, who do not arrive until December and appear to leave more quickly after spawning.

The red gurnard enters the western and central English Channel in September, and remains from November to January in an area between Ushant and the Isle of Wight, particularly around the Central Trough.

The red gurnard is an active hunter, using the three free rays of its pectoral fins to "walk" on the bottom and search for its prey. By using these fin rays, the rest of the pectoral and the pelvic fins remain free for rapid use to escape or to hunt. It is a carnivorous predator that feeds on crustaceans (hermit crabs, prawns, crabs) and various small benthic fish such as gobies and dragonets. Juveniles feed almost exclusively on crustaceans, while adults have a mixed diet of fish and crustaceans.

Description of the otolith

Oval-shaped, with prominent *rostrum* and *antirostrum*. Both are on the posterior margin. Lobed margins with a pronounced angle between the posterior and dorsal margins. Ventral margin very curved with an angle in the centre. The oval *cauda* and funnel-shaped *ostium* are of equal length. Medium to large in size compared to other species of the same size.

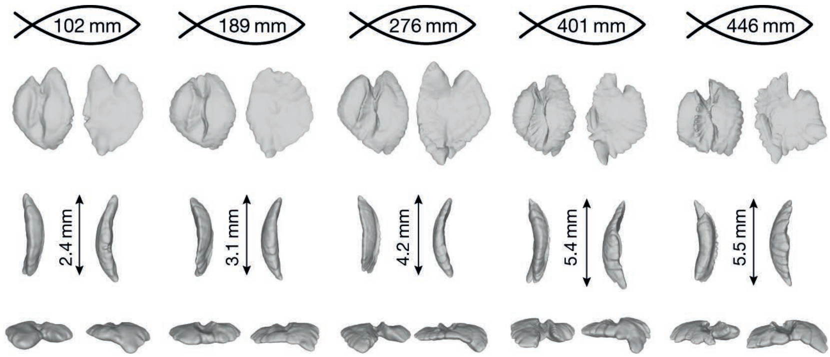


Figure 35. Changes in otolith shape and size over the lifetime of the red gurnard, represented by five individuals identified by their total length expressed in millimetres.

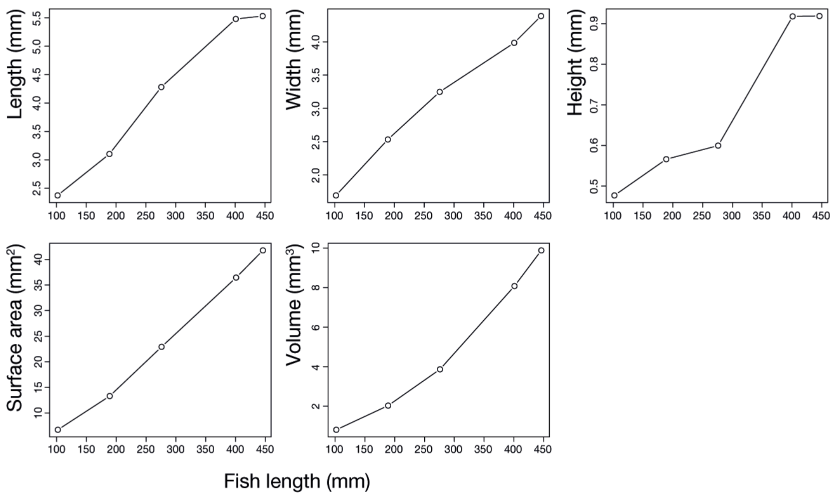


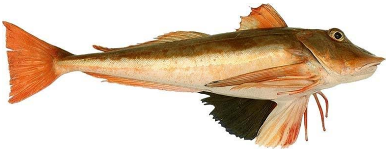
Figure 36. Relationships between otolith morphology and length in red gurnard.

Summary

The fish analysed measured between 10 and 45 cm, with otoliths between 2.4 and 5.5 mm long. This shows that the otolith grows more slowly than the fish. During the life of the red gurnard, the shape of the otolith evolves, with a rounded edge that tends to become serrated, and the *sulcus* becomes deeper. Unlike the other individuals, the 18.9 cm fish shows a shallow area between the *rostrum* and the *antirostrum*. Only some individuals show this shallowness, so this area should not be used to discriminate this species.

Tub gurnard

Latin name: *Chelidonichthys lucerna*
Order: Perciformes
Family: Triglidae
Morphotype: round fish



Distribution area

The tub gurnard is found in the North-East Atlantic, from northern Norway to Senegal. It is also found in the Mediterranean and Black Seas.

Environment

A benthic fish living on bottoms between 0 and 300 m deep and at temperatures between 8 and 24 °C, it is mainly found on seabeds composed of sand, muddy sand and gravel on the continental shelf.

Biology and life cycle

The tub gurnard, beginning from 18 cm long, breeds from December to February in the Mediterranean and from May to June in the Celtic Sea. In summer, the young regroup with the adults at the coast. Young individuals have previously been identified in estuaries such as the Gironde. In winter, the tub gurnard migrates to deeper waters.

It is a carnivorous predator. Young individuals smaller than 15 cm feed mainly on copepod crustaceans, then their diet evolves towards mysids, shrimps and amphipods. From 20 cm upwards, the prey consists of fish and a few cephalopod molluscs.

Description of the otolith

Elliptical in shape, with prominent *rostrum* and *antirostrum*. *Rostrum* broad and pointed. *Antirostrum* also pointed but thinner. Margins narrow with a pronounced angle in the centre of the dorsal margin. The *cauda* is shorter than the *ostium*, broad, oval and closed; the *ostium* is open. The *ostium* and *cauda* are deep. Medium-sized compared to other species of the same size.

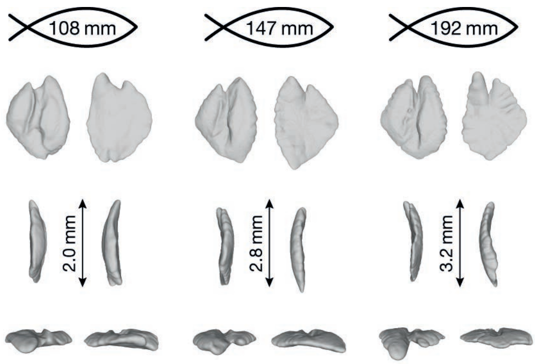


Figure 37. Changes in otolith shape and size during the life of the tub gurnard, represented by three individuals identified by their total length expressed in millimetres.

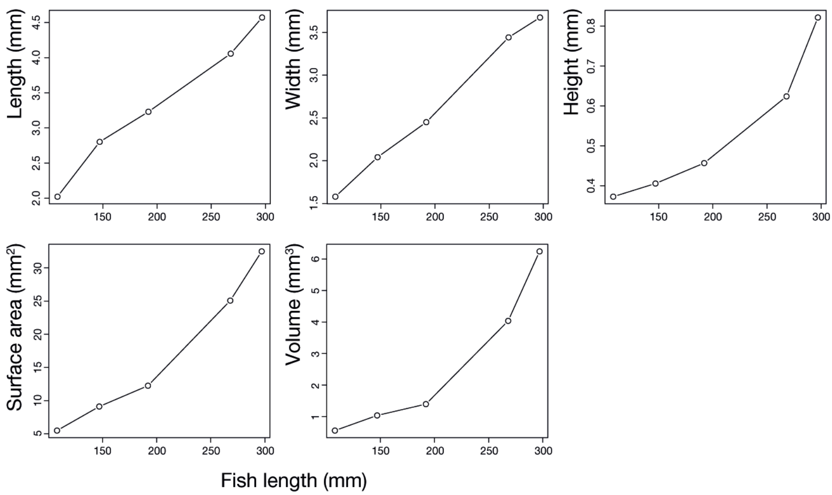


Figure 38. Relationships between otolith morphology and length in tub gurnard.

Summary

The fish analysed measured between 10 and 20 cm, with otoliths between 2 and 3.2 mm long. This shows that the otolith grows at a relatively similar rate to the fish. During the life of the tub gurnard, the shape of the otolith remains very comparable from one individual to another, as clearly shown by the relationships between the different morphological criteria and the size of the fish.

Striped red mullet

Latin name: *Mullus surmuletus*
Order: Mulliformes
Family: Mullidae
Morphotype: round fish

Distribution area

The striped red mullet is found along European coasts from southern Norway and northern Scotland, including the Faroe Islands, to the Strait of Gibraltar, but also in the northern part of West Africa, in the Mediterranean basin and in the Black Sea.

Environment

A benthic fish with a gregarious nature, this species frequents sandy, gravelly and rocky bottoms. In the Bay of Biscay, this fish is also found on shellfish beds, eelgrass beds and in rocky channels. It is most abundant in waters no deeper than 100 m.

Biology and life cycle

The striped red mullet reaches its first sexual maturity at 17 cm in the Channel and the Bay of Biscay. Spawning takes place between April and June in the Bay of Biscay and from May to July in the eastern Channel. The juveniles begin their benthic life close to the coast at depths of 15 to 20 m, right up to the extreme margin, as they have been observed in less than 50 cm of water in calm conditions. During their first winter, juveniles migrate from their nurseries to deeper waters, where they spend their adult lives.

The striped red mullet is a carnivorous fish. The anatomy of this species, with its two chin barbels, gives it a mixed predatory behaviour: it is a sight hunter (crustaceans and fish), a browser, and a burrower (bivalves and worms). In addition, the presence of sediment in the stomachs and the nature of the prey ingested show the close link between the animal and the seabed.

In the North-East Atlantic Ocean, there are two populations: one from the south of the western Channel with the Celtic Sea and the Bay of Biscay, and the other from the eastern Channel to the north of the North Sea.

Description of the otolith

Oval-shaped, with a fairly prominent *rostrum* and a small *antirostrum*. Margin very irregular. The *cauda* is longer than the funnel-shaped *ostium*, very curved towards the ventral margin, and closed. Quite large compared to other species of the same size.

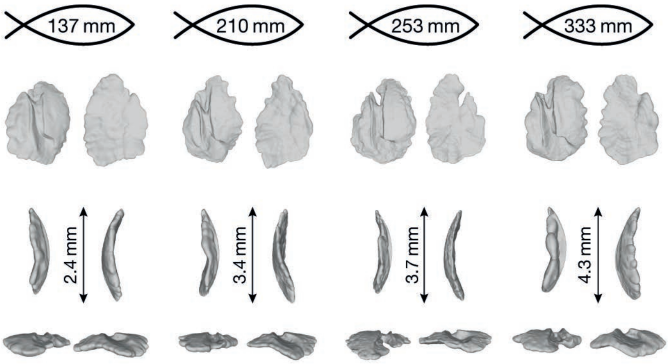


Figure 39. Changes in otolith shape and size over the lifetime of the striped red mullet, represented by four individuals identified by their total length expressed in millimetres.

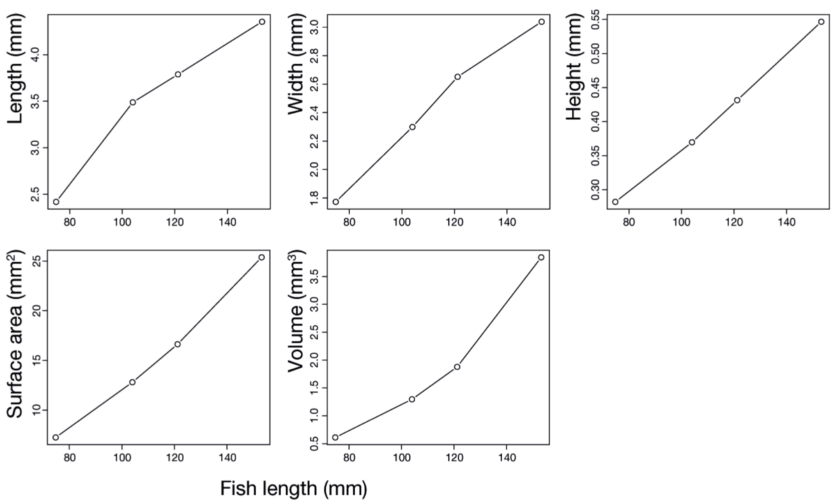


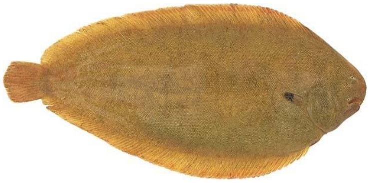
Figure 40. Relationships between otolith morphology and length in striped red mullet.

Summary

The fish analysed measured between 13 and 34 cm, with otoliths between 2.4 and 4.3 mm long. This shows that the otoliths grow at a relatively similar rate to the fish. The evolution of the otolith over the lifetime of the striped red mullet shows that it is essentially the anterior part that changes, with the *sulcus* deepening and widening with the size of the fish. Some otoliths (but not all) can have a *sulcus* so deep in the anterior part that the *ostium* forms a hole in the otolith in both internal and external views.

Common sole

Latin name: *Solea solea*
Order: Pleuronectiformes
Family: Soleidae
Morphotype: flatfish



Distribution area

Common sole live in the continental waters of the North Atlantic, from the Shetlands and southern Norway in the north to Mauritania in the south. It is absent from the Baltic and certain regions of the Mediterranean and Black Sea.

Environment

A benthic fish living on fine sandy or muddy bottoms between 0 and 150 m deep. The common sole is very eurythermal and euryhaline, meaning it can withstand wide variations in temperature and salinity, enabling juveniles to live inside estuaries or bays.

Biology and life cycle

Common sole reach sexual maturity between 25 and 30 cm, i.e. when they are three years old. Spawning begins when the water temperature rises above 7 °C. Consequently, reproduction takes place in the English Channel and North Sea from late February to late June, with a peak period in April-May. In the eastern Channel, the highest concentrations of common sole eggs have been observed in the Pas-de-Calais Strait, in the Bay of Seine and around the Isle of Wight.

Larvae can travel several dozen kilometres to reach their nurseries. Larvae undergoing metamorphosis change their vertical and horizontal distribution, concentrating near the bottom and in the coastal zone. Once they have metamorphosed, the juveniles, which resemble adults, have a benthic lifestyle. They aggregate in bays and estuaries, specifically selecting soft muddy and sandy bottoms generally shallower than 20 m.

Common sole are largely nocturnal opportunistic predators, whose diet consists of benthic and epibenthic invertebrate fauna that are sessile or not very mobile.

Description of the otolith

Mostly oval to round. Margins smooth. Posterior margin convex with marked, and sometimes prominent, angles between the dorsal and ventral margins. *Rostrum* not marked, *antirostrum* absent. The *sulcus* is deep, present over about 75% of the otolith, and fairly linear. The *cauda* is much shorter than the *ostium* and both are closed. The interior is convex. Medium-sized compared to other species of the same size.

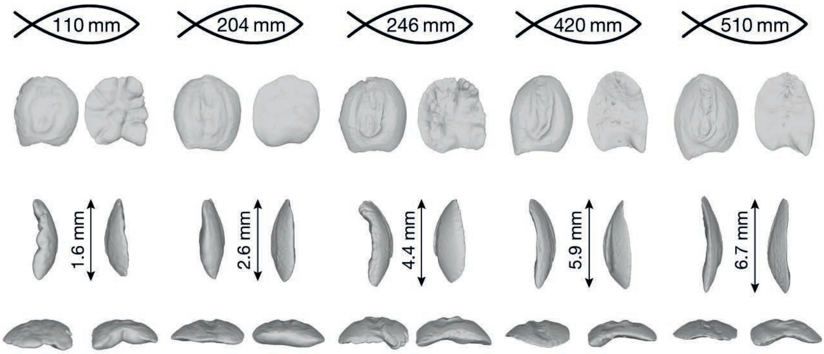


Figure 41. Changes in otolith shape and size during the life of the common sole, represented by five individuals identified by their total length expressed in millimetres.

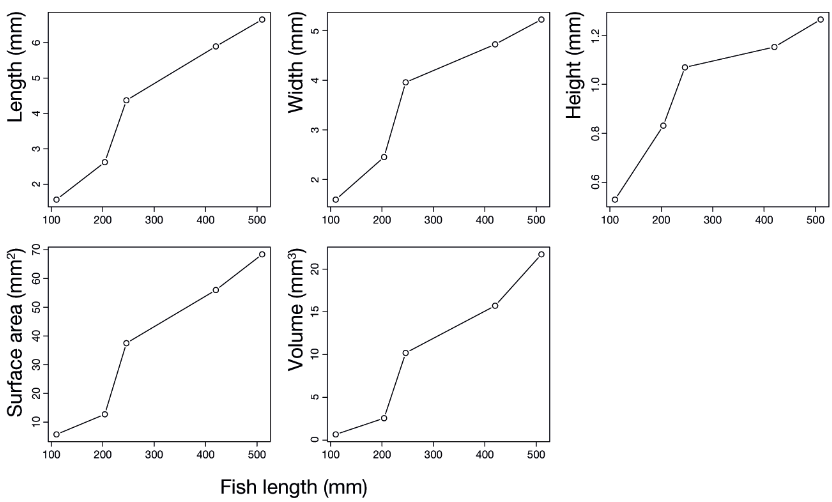


Figure 42. Relationships between otolith morphology and length in common sole.

Summary

The fish analysed measured between 11 and 51 cm, with otoliths ranging in length from 1.6 to 6.7 mm. This shows that the otoliths grow at a similar rate to the fish. In common sole, the otolith is always marked by an asymmetry of the proximal inner surface. The *sulcus*, which is very wide and shallow in young individuals, becomes deeper and narrower in adults. Similarly, the width/length ratio decreases over time, as the otolith grows more rapidly along the anterior-posterior axis than along the dorso-ventral axis. The lobes present on the distal external surface may diminish, or even disappear, during the life of the fish.

Lemon sole

Latin name: *Microstomus kitt*
Order: Pleuronectiformes
Family: Pleuronectidae
Morphotype: flatfish

Distribution area

The lemon sole is found on the continental shelf in the North-East Atlantic, from the White Sea and Iceland to the Bay of Biscay. It is common in the North Sea and English Channel, but absent from the Baltic Sea.

Environment

A benthic fish living on hard seabeds (rocky plateaux), gravels or shellfish beds, from the coast to a depth of 200 m. Juvenile lemon sole in the Western Channel are distributed over hard bottoms at depths of 50 to 100 m.

Biology and life cycle

The lemon sole reaches its first sexual maturity between three and six years of age, corresponding to a size of between 12 and 30 cm. Breeding takes place from January to March in the Bay of Biscay, from April to July in the west of the British Isles, from May to August in the Faroe Islands and Iceland, and from May to September in the northern North Sea, at a depth of around 100 m. In the western Channel, the females lay their eggs from March to August, with a peak from May to June. The eggs and larvae are pelagic, and the juveniles move into the benthic phase only after metamorphosis. Unlike most flatfish, lemon sole juveniles grow in the deep waters of the eastern Channel.

The lemon sole does not migrate during its life in the Western Channel. However, this species does migrate seasonally off the coast of Scotland.

Lemon sole feed mainly on annelid polychaetes, small crustaceans, molluscs, echinoderms, coelenterates, nemerteans and ascidians. Over the course of its life, its interest in annelid polychaetes diminishes in favour of crustaceans and coelenterates. Additionally, lemon sole stop feeding completely during the winter.

Description of the otolith

Mostly rectangular to oval. Smooth margins. *Rostrum* and *antirostrum* sometimes prominent, *antirostrum* sometimes absent. *Sulcus* deep, straight and closed at the end of the *cauda*. Ridges or concretions are sometimes present around the *sulcus*. Medium size compared to other species of the same size.

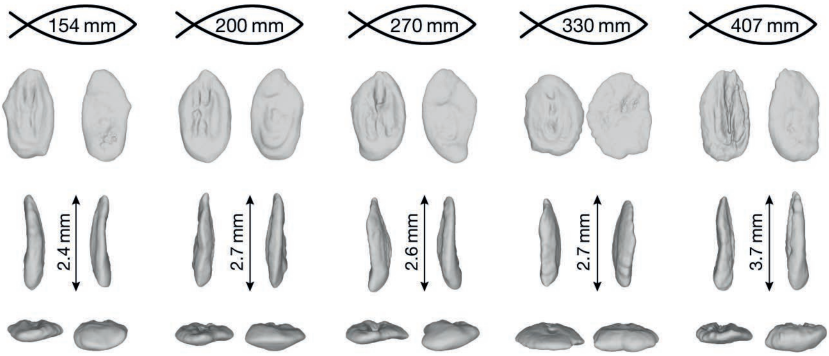


Figure 43. Changes in otolith shape and size over the lifetime of the lemon sole, represented by five individuals identified by their total length expressed in millimetres.

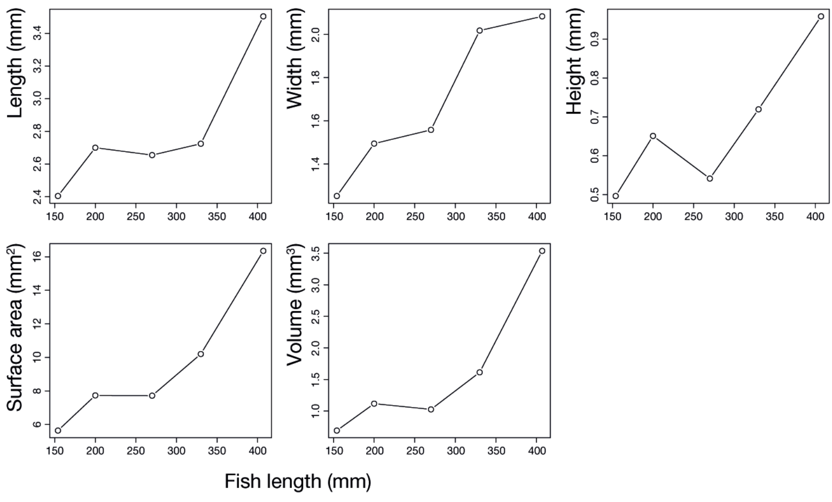


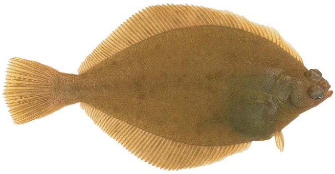
Figure 44. Relationships between otolith morphology and length in lemon sole.

Summary

The fish analysed measured between 15 and 41 cm, with otoliths between 2.4 and 3.7 mm long. This shows that the otolith grows more slowly than the fish. In lemon sole, as in other flatfish, otoliths evolve, for fish between 15 and 30 cm, with a relatively elongated shape with a pronounced *rostrum* and a shallow *sulcus*. For fish over 35 cm, the otolith takes on its final shape with an asymmetrical proximal inner surface and an increasing width/length ratio. The *rostrum* becomes flatter and the *sulcus* deeper.

Common dab

Latin name: *Limanda limanda*
Order: Pleuronectiformes
Family: Pleuronectidae
Morphotype: flatfish



Distribution area

The common dab is found in the North-East Atlantic, from northern Norway and Iceland to the Bay of Biscay, and in the Barents, White and Baltic Seas.

Environment

A benthic fish living on sandy bottoms 20 to 150 m deep, this northern species is distributed in marine waters with temperatures between 0 and 18 °C. This species seems to thrive in shallow areas, protected from strong tidal currents and with muddy sediments.

Biology and life cycle

The common dab begins to reproduce between 10 and 20 cm. In the English Channel and southern North Sea, reproduction takes place from February to April on fine to coarse sand at depths of 20 to 40 m. The pelagic eggs hatch after three to 14 days incubation, depending on the temperature. The pelagic larvae metamorphose in May-June at around 12-13 mm and migrate towards the seabed and the coast. In the eastern Channel, nurseries are distributed in the Veys, Seine, Somme, Canche, Authie, Rye and Solent bays. The fry spend their first year at a depth of between 8 and 10 m, before moving away from the coast.

Adult common dab feed on small crustaceans, bivalve molluscs, annelids, echinoderms, cnidarians and a few small fish.

Description of the otolith

Mostly oval in shape. Relatively rectangular with a rather smooth edge. The *ostium* is longer than the *cauda*, and the two are separate and closed.

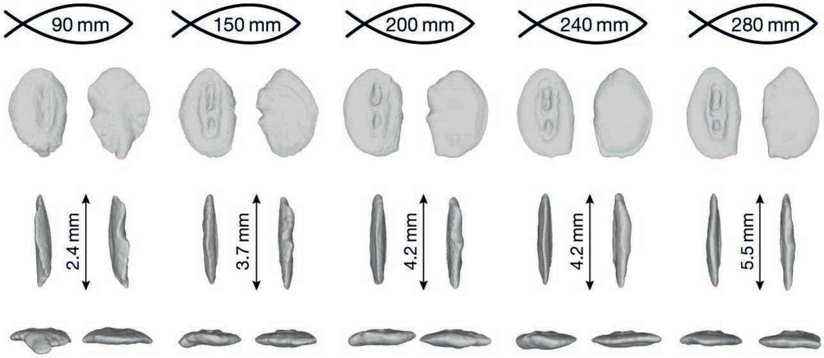


Figure 45. Changes in otolith shape and size over the lifetime of the common dab, represented by five individuals identified by their total length expressed in millimetres.

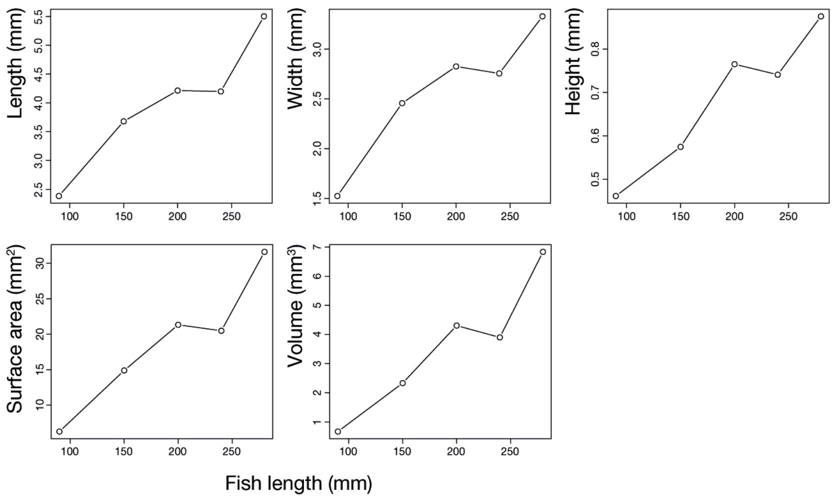


Figure 46. Relationships between otolith morphology and length in common dab.

Summary

The fish analysed measured between 9 and 28 cm, with otoliths between 2.4 and 5.5 mm long. This shows that the otolith grows more slowly than the fish. The evolution of the otolith is particularly noticeable early in the life of common dab, with the shape of the proximal inner surface becoming simpler and the *sulcus*, inversely, forming and becoming hollow. For fish larger than 20 cm, the distal external surface becomes much flatter.

European flounder

Latin name: *Platichthys flesus*
Order: Gadiformes
Family: Gadidae
Morphotype: flatfish

Distribution area

The European flounder is very common in the eastern Atlantic, particularly in the coastal and brackish waters of western Europe, and found from the White Sea to the Mediterranean and Black Seas. It is also found around the coasts of the United States and Canada, as this species was accidentally introduced via ballast water.

Environment

A benthic fish that lives on sandy, sandy-muddy and muddy bottoms between the coast and a depth of 60 m, although it can also be found at depths of up to 100 m. It is a ubiquitous fish, found mainly in coastal marine waters and estuaries, but can also live in brackish or even fresh waters when it swims up rivers. This species is highly tolerant of wide variations in salinity. The European flounder can also adapt to a wide range of temperatures, from polar to temperate climates. In the English Channel, it is found mainly in estuaries and coastal waters along the English and French coasts.

Biology and life cycle

European flounder spend the summer in rivers and estuaries, returning to the sea in winter to spawn, with a spawning period lasting from January to August. Spawning begins in mid-January in the southern North Sea, continuing until April in the south of its range and until August in the north. The eggs are pelagic and spherical. The larvae develop in estuarine or peri-estuarine waters. The European flounder migrates to slightly deeper waters with sandy-muddy bottoms at sexual maturity.

Description of the otolith

Oval-shaped, with a prominent, relatively serrated *rostrum*. No *antirostrum*. Pronounced angle between posterior and dorsal margin. Slightly convex proximally and fairly flat distally. The *sulcus* is short, straight and closed on both sides. Fairly large compared to other species of the same size.

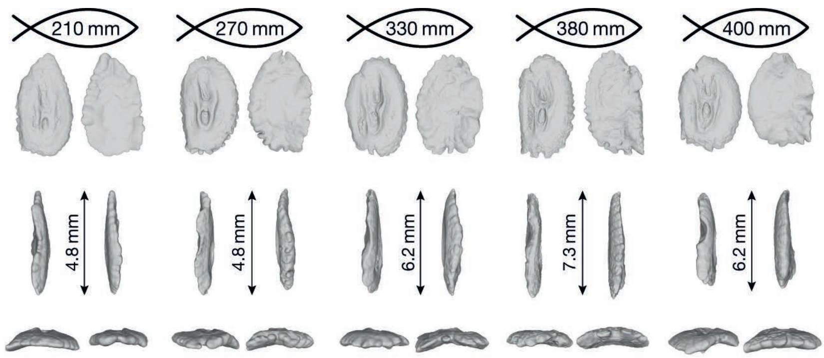


Figure 47. Changes in otolith shape and size during the life of the European flounder, represented by five individuals identified by their total length expressed in millimetres.

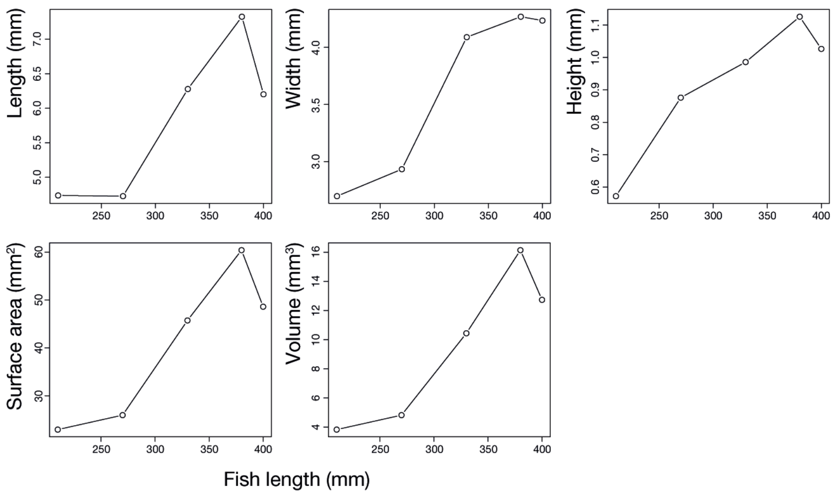


Figure 48. Relationships between otolith morphology and length in European flounder.

Summary

The fish analysed measured between 21 and 40 cm, with otoliths ranging in length from 4.8 to 7.3 mm. This shows that the otolith grows more slowly than the fish. Only the 21 cm European flounder shows a well-marked *rostrum* at the tip. Later in the life of the European flounder, however, all the otoliths show a rounded area at the *rostrum* and an antero-posterior asymmetry, with a lobed dorsal side and a straight ventral side.

Turbot

Latin name: *Scophthalmus maximus*
Order: Pleuronectiformes
Family: Scophthalmidae
Morphotype: flatfish

Distribution area

The turbot is found in the North-East Atlantic, throughout the Mediterranean Sea and along the European coast as far north as the Arctic Circle. It is also very common in most of the Baltic Sea.

Environment

A bentho-demersal fish, living on sandy, rocky or mixed seabeds. Turbot are fairly common in brackish waters.

Biology and life cycle

Turbot reproduce from a length of 40 to 45 cm, between February and April in the Mediterranean, and from May to July in the Atlantic. Eggs are laid sequentially every two to four days. The female produces pelagic eggs. The larvae are initially symmetrical but, at the end of metamorphosis, between 40 to 50 days after hatching, the right eye moves to the left, losing the initial bilateral symmetry.

The turbot feeds mainly on other, often small, bottom-dwelling fish, and also, to a lesser extent, on crustaceans and bivalves.

Description of the otolith

Mostly oval to rectangular in shape, and more elongated than that of *Scophthalmus rhombus*. Margins crenelated. Angle between anterior and dorsal margins marked. *Rostrum* broad and rounded, *antirostrum* rather small or absent. The linear *sulcus* is present on about 75% of the otolith. The *cauda* measures a third of the length of the *ostium*. Fairly large compared with other species of the same size.

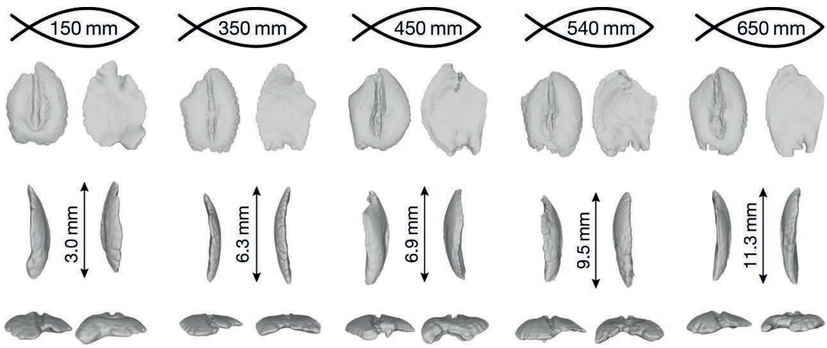


Figure 49. Changes in otolith shape and size over the lifetime of the turbot, represented by five individuals identified by their total length expressed in millimetres.

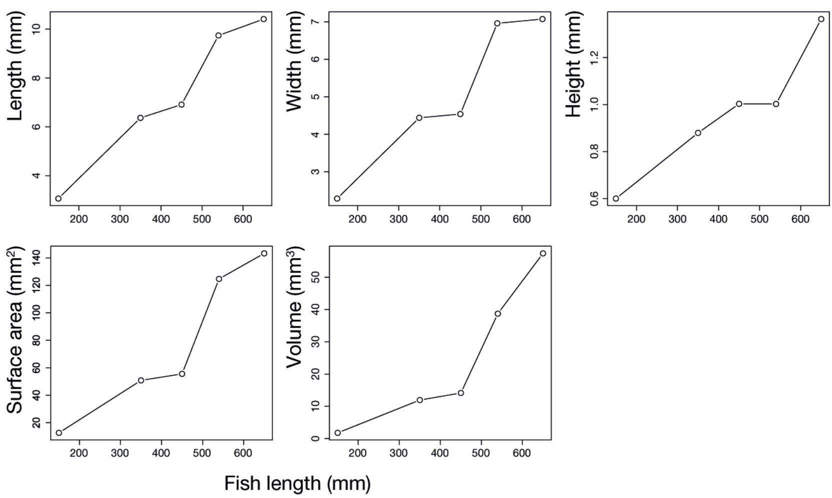


Figure 50. Relationships between otolith morphology and length in turbot.

Summary

The fish analysed measured between 15 and 65 cm, with otoliths ranging in length from 3 to 11.3 mm. This shows that the otoliths grow in a similar way to the fish. In turbot, as in other flatfish, for fish between 15 and 40 cm, otoliths evolve with a relatively elongated shape, with a pronounced *rostrum* and a shallow *sulcus*. For fish over 40 cm, the otolith takes on its final shape with an asymmetrical proximal inner surface and increasing height. The *sulcus* deepens as the fish grows.

European plaice

Latin name: *Pleuronectes platessa*
Order: Pleuronectiformes
Family: Pleuronectidae
Morphotype: flatfish

Distribution area

European plaice are widely distributed throughout the continental waters of the North Atlantic, from Greenland and the White Sea to the coast of North Africa. Channel plaice move into the North Sea and vice versa.

Environment

A bentho-demersal fish living preferentially on sandy, but also gravelly or muddy seabeds, from the coast to a depth of 200 m. European plaice are found in saline to brackish temperate waters.

Biology and life cycle

European plaice reach their first sexual maturity at an average age of two to four years, with sizes ranging from 20 to 33 cm in the southern North Sea. The average size at first maturity, which varies greatly from one individual to another, is 25 cm for males and 31-33 cm for females, and takes place around the age of three in the English Channel. Here, European plaice reproduce from December to March, with a peak generally in January-February. They reproduce where they were born, and spawning grounds are located in the centre of the Channel. The eggs and larvae are pelagic and carried by the current. After metamorphosis, the juveniles arrive at the coastal nurseries thanks to the tidal currents, positioning themselves in the open water when the tide rises before returning to the bottom at slack water and remaining there throughout the ebb tide. Such movement mechanisms are also used by adults during breeding and feeding migrations.

The European plaice feeds on benthic prey throughout its life. Preferred prey are bivalve molluscs and, to a lesser extent, annelid polychaetes. Adult plaice may eat some small fish.

Description of the otolith

Mostly oval in shape, with a prominent angle between the posterior and dorsal margins. The dorsal margin is fairly linear. The *rostrum* is rounded. The *anti-rostrum* is absent. The *sulcus* is shallow and extends over 50% of the length. The *ostium* is longer than the *cauda*, and both are closed. Quite large compared to other species of the same size.

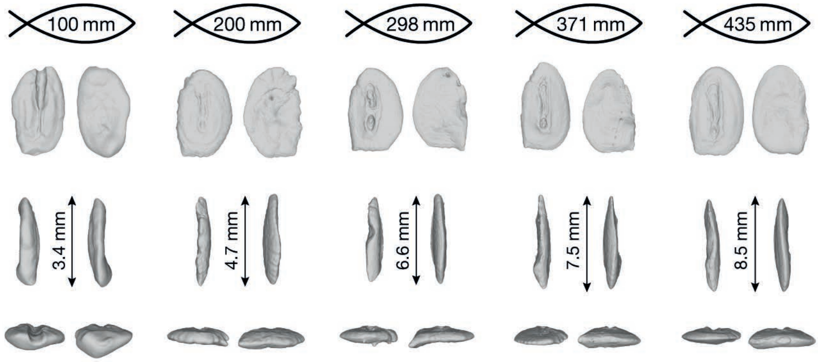


Figure 51. Changes in otolith shape and size during the life of the European plaice, represented by five individuals identified by their total length expressed in millimetres.

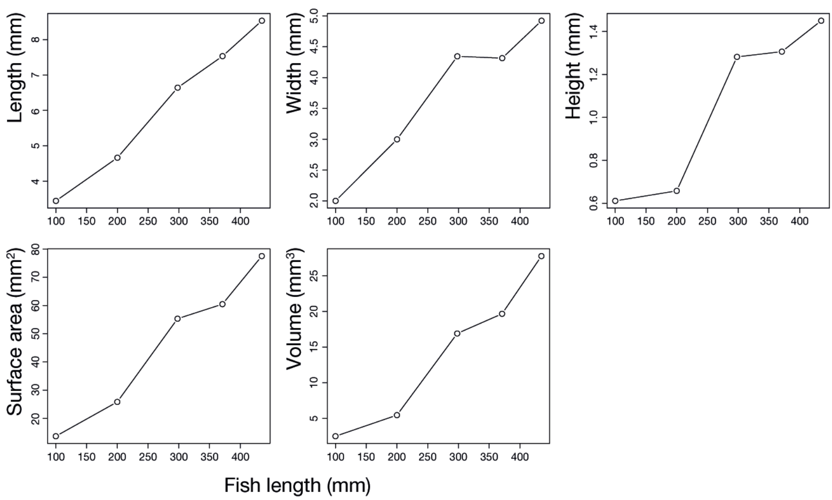


Figure 52. Relationships between otolith morphology and length in European plaice.

Summary

The fish analysed measured between 10 and 44 cm, with otoliths between 3.4 and 8.5 mm long. This shows that the otolith grows at a much slower rate than the fish. A 10 cm fish has a very different otolith to larger fish, with an open *sulcus* at the front and a relatively rectangular shape. From 20 cm onwards, the otolith takes on its final shape with an asymmetry of the proximal inner surface; the *sulcus* deepens in the centre of the otolith and is no longer open.

Brill

Latin name: *Scophthalmus rhombus*
Order: Pleuronectiformes
Family: Scophthalmidae
Morphotype: flatfish

Distribution area

The brill is found in the North-East Atlantic, from 68° north to Morocco, and particularly in Iceland. It is also known throughout the Mediterranean and Black Seas.

Environment

A bentho-demersal fish that lives only on sandy or mixed seabeds.

Biology and life cycle

Brill reach their first sexual maturity between 25 and 37 cm, with a big difference in size between the females and the much smaller males. The breeding season takes place between March and August.

Brill feed on fish and crustaceans.

Description of the otolith

Mostly elliptical to oval. *Rostrum* wide and sometimes prominent, *antirostrum* rather small or absent. The deep *sulcus* is present over about 75% of the otolith. The *cauda* is one third the size of the *ostium*. Medium to large in size compared with other species of the same size.

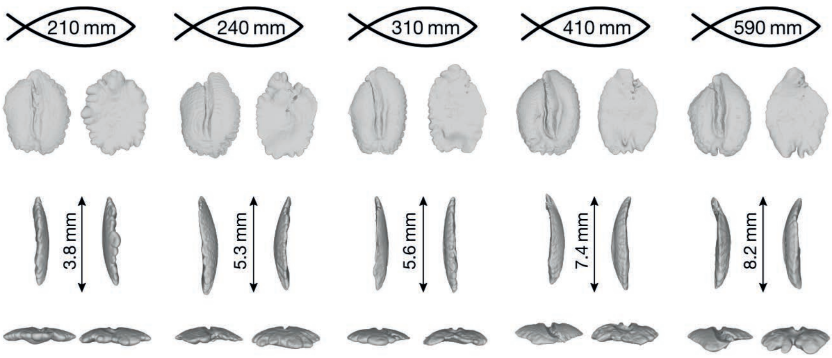


Figure 53. Changes in otolith shape and size during the life of the brill, represented by five individuals identified by their total length expressed in millimetres.

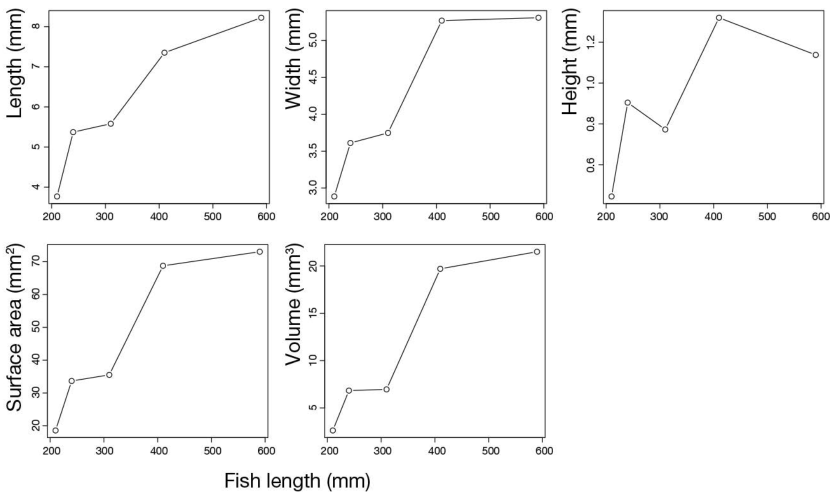


Figure 54. Relationships between otolith morphology and length in brill.

Summary

The fish analysed measured between 21 and 59 cm, with otoliths ranging in length from 3.8 to 8.2 mm. This shows that the otolith grows at a slightly slower rate than the fish. In the brill, unlike other flatfish, the smallest fish have a flattened *rostrum* that becomes thinner as they grow. Similarly, the indented outline of the otoliths of juveniles becomes smoother as they grow. Finally, as with many flatfish, the otolith has an asymmetrical proximal inner surface and a relatively deep but narrow *sulcus*.

Species identification criteria

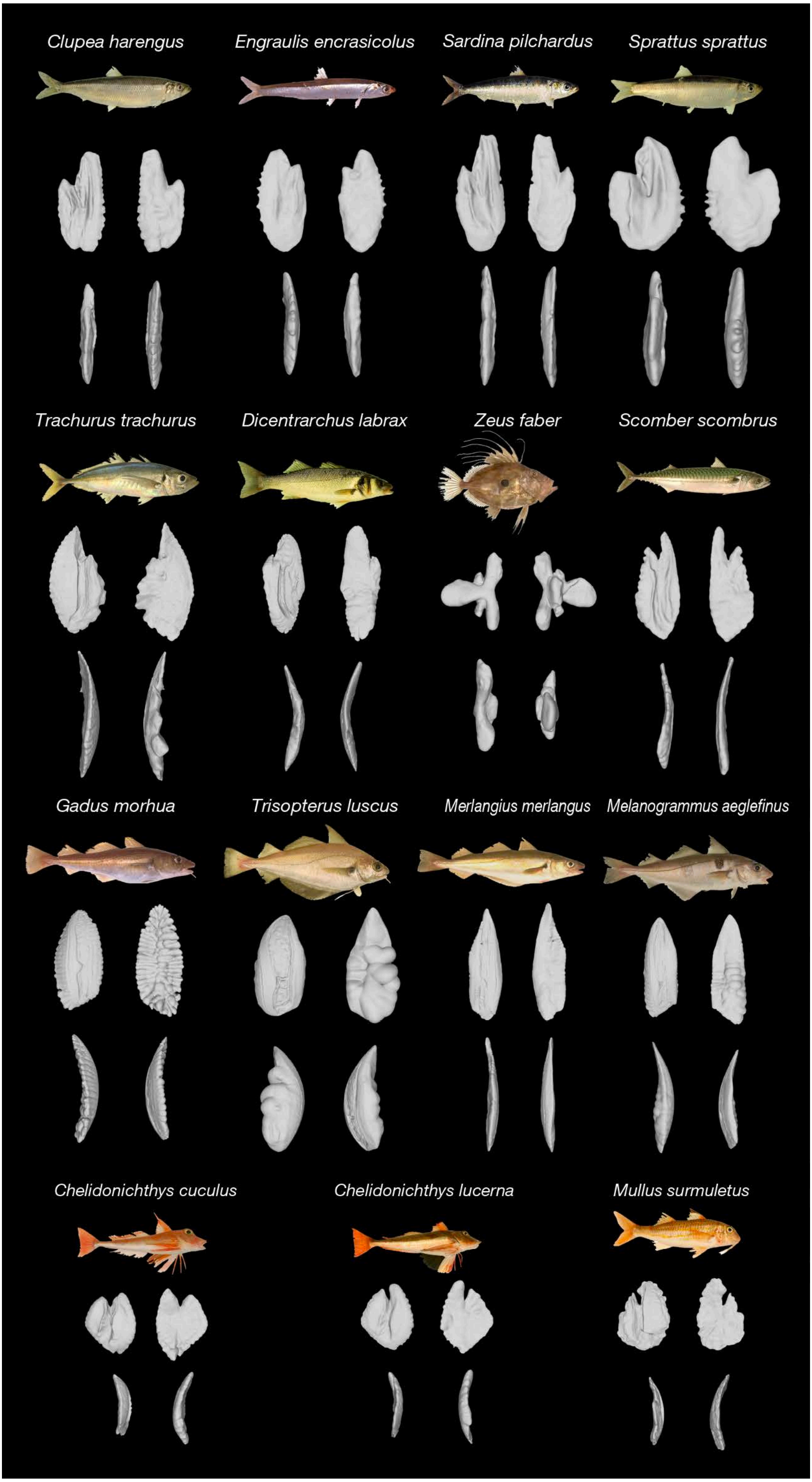
The main morphological criteria of an otolith are numerous and include the nature and complexity of its outline, its general shape (round, oval, rectangular, etc.), the convexity of the proximal inner surface, the concavity of the distal outer surface and, finally, the thickness that can be measured in ventral and dorsal views. To compare these measurements of concavity, convexity and thickness, the ventral view is used, as it has a less indented and less variable edge than the dorsal view, where the lobed parts of the otolith are generally located. Thus, the dorsal view is one of the last criteria used to recognise the species, while the internal surface in proximal view is often the first observation used to determine the species, as it provides a good view of the edge, but also of the part called the *sulcus acusticus* where the membrane attaches to the otolith. This area is extremely informative, and discriminant in identifying the species to which the analysed otolith belongs. This *sulcus acusticus* is relatively central to the internal face, and oriented along an antero-posterior axis starting near the posterior edge with a zone called the *cauda*, then continuing with a second zone called the *ostium* and finally ending at the anterior edge called the *excisura*. This *excisura* is extremely important, as it connects the *rostrum* to the *antirostrum*, and this zone is particularly distinguishable between species that are often very close in terms of taxonomy. While the proximal inner surface provides a great deal of morphological information, the distal outer surface can add significantly to the morphological criteria with the presence of more or less numerous lobes.

Of the 22 main commercial species of fish in the Channel and North Sea (Figure 55), the John Dory is the easiest species to identify, as it is the only one to have an atypical “star” shape, due to the existence of a posterodorsal ridge. The general shape is the first criterion to be observed, because otoliths show shapes in proximal and distal views that can range from round to square, passing through a rectangle or elongated shape (known as oblong), which ultimately translates into a ratio between the length and width of the otolith.

The second criterion for identifying the species is the presence of the *rostrum* and the *antirostrum*, separated by a marked *excisura* (anterior part at the level of the *sulcus*), and showing an indentation in the shape. This is observed in certain round fish in particular, such as mackerel, anchovy, herring, sprat, pilchard, red and tub gurnards and striped red mullet. Conversely, almost none of the flatfish have this anatomical feature. The characteristics of the *sulcus* are also extremely helpful for identifying species. It is useful to investigate the ratio between its size and that of the anterior-posterior axis: 1:1 in mackerel, horse mackerel and cod; 2:3 in pilchard, haddock, turbot and brill; and 1:3 in common dab and sprat, for example. In addition to its size, the *sulcus*, made up of the *cauda* and *ostium*, shows either continuity between these two areas forming a single groove (in mackerel, gurnard and sole), or two well-separated grooves on the antero-posterior axis (in dab, lemon sole and plaice). Finally, the *sulcus* can be an indicator of the species based on the width and depth of its grooves.

Another criterion that can be observed on the proximal inner surface is complexity of the outer shape, which may include lobes. These contour shapes are either absent (in sole, dab and plaice), lobed (in cod, whiting and turbot, for example), or serrated (in anchovy, flounder, sprat, and red and tub gurnard, for example).

On the distal external face, there may also be lobed bulges or lumps present on the face and not on its contour (in pouting and cod, for example). While the proximal internal and distal external faces are used primarily to distinguish the first criteria for identifying the species, it is also necessary to use the ventral and dorsal views to observe the concavity, which may be very pronounced (in seabass, red and tub gurnard and striped red mullet, for example) or, conversely, virtually absent (in dab, plaice, herring and sprat, for example). The second criterion to be observed on these faces is the thickness of the otolith, reflecting its height, which is either great (in pouting, sprat and John Dory, for example) or thin (in whiting and mackerel, for example).


Clupea harengus
Engraulis encrasicolus
Sardina pilchardus
Sprattus sprattus
Trachurus trachurus
Dicentrarchus labrax
Zeus faber
Scomber scombrus
Gadus morhua
Trisopterus luscus
Merlangius merlangus
Melanogrammus aeglefinus
Chelidonichthys cuculus
Chelidonichthys lucerna
Mullus surmuletus

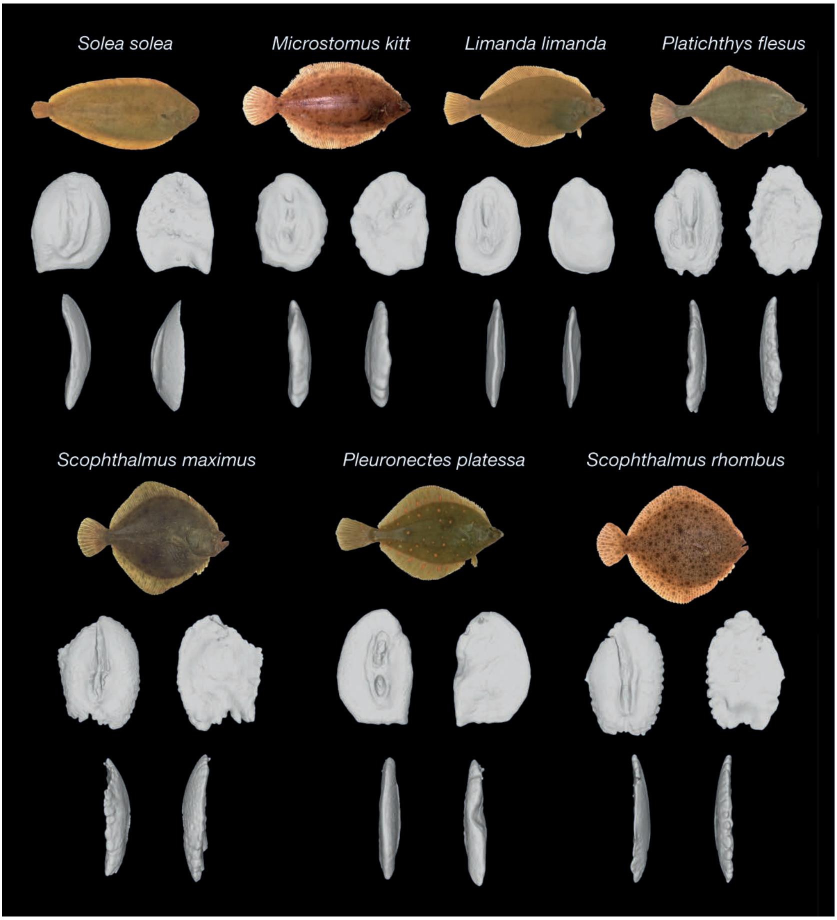


Figure 55. Presentation of the otoliths of the 22 main Channel-North Sea species with the four 2D views extracted from the 3D image.

A principal component analysis using the individual 3D Fourier coefficients from the Spharm analysis was carried out to visualise the differences and similarities in shape between the species. Figures 56 and 57 show the projection of individuals onto the first four principal components of the PCA, which summarise more than 60% of the variations in shape contained in the coefficients. These graphical analyses make it possible to understand the differences between species, but also to see which species are closest to that identified as the most likely, and to refine our judgement if necessary.

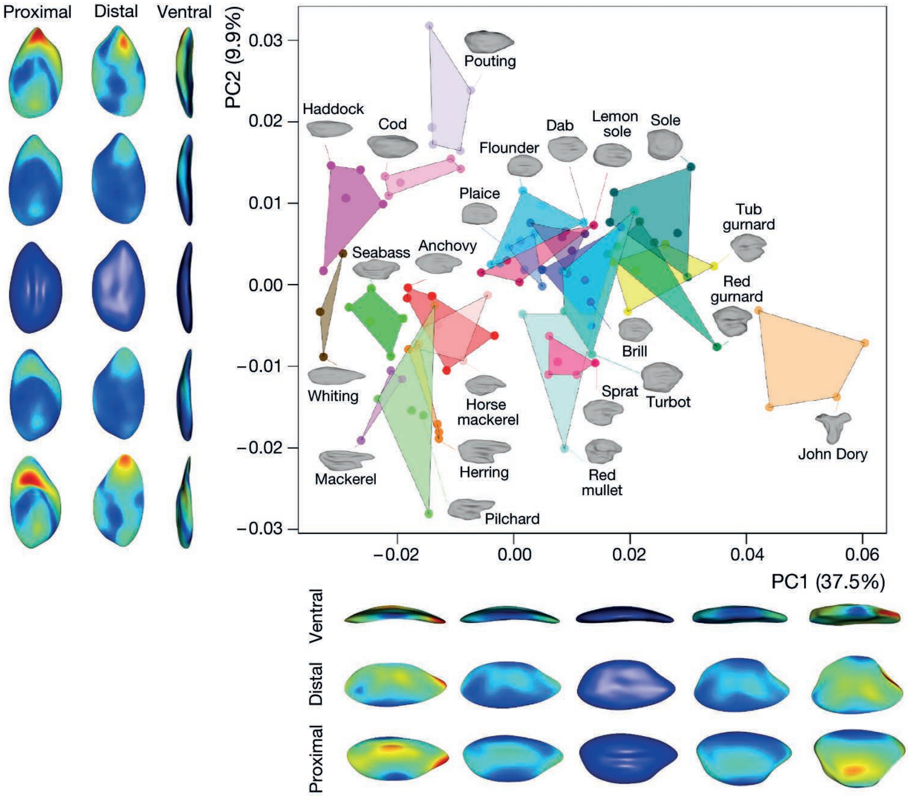


Figure 56. Graphical representation of principal components PC1 and PC2 of the differences between the 3D shape of the otoliths for the 22 main Channel-North Sea species.

Each individual analysed is represented by a coloured point, and all individuals of a species are delimited by a convex envelope (polygon). The theoretical shape for each species has been reconstructed to help visually understand the morphological criteria that bring certain species together. To illustrate the differences that explain each graphical axis, termed the PC, three views (proximal, distal and ventral) are shown, colour-coded from dark blue (no difference) to red (greatest difference).

The first graphical axis (PC1) is explained essentially by the central zone representing the *sulcus* (Figure 56). Axis PC2 clearly shows that the *rostrum* and *antirostrum* area, with the *excisura* in the middle, is a very important criterion for species discrimination. Finally, the graphical axes PC3 and PC4 indicate differences in all views, and in particular within views and not just on the outer contour of the proximal view used conventionally in 2D analysis (Figure 57).

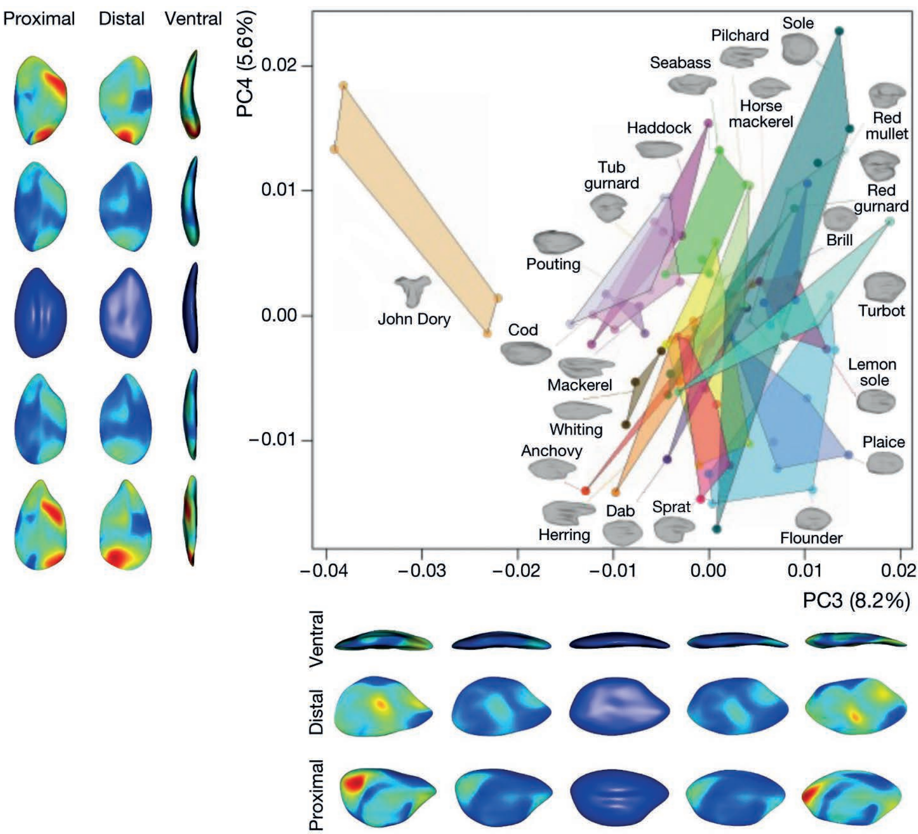


Figure 57. Graphical representation of principal components PC3 and PC4 of the differences between the 3D shape of the otoliths for the 22 main Channel-North Sea species.

Each individual analysed is represented by a coloured point, and all individuals of a species are delimited by a convex envelope (polygon). The theoretical shape for each species has been reconstructed to help visually understand the morphological criteria that bring certain species together. To illustrate the differences that explain each graphical axis, termed the PC, three views (proximal, distal and ventral) are shown, colour-coded from dark blue (no difference) to red (greatest difference).

Otolith shape linked to habitat and morphotype

Otoliths enable fish to detect auditory and vestibular stimuli (Wright *et al.*, 2002). The science of ecomorphology is based on the fact that shape is the result of functional adaptation to the environment (Feilich and López-Fernández, 2019). Due to the low level of visibility in relation to the surface, demersal species (fish living in the middle of the water column) and benthic species (species living on the seabed), have much more developed hearing than pelagic species (species living at the top of the water column, closer to the surface) (Lychakov and Rebane, 2005; Wright *et al.*, 2010). An ecomorphology study based on fish species observed between 200 and 750 m below the surface demonstrated that there is a positive correlation between depth and otolith size (Cruz and Lombarte, 2004; Lombarte and Cruz, 2007). The relationship between otolith shape and size and the functions of mechanoreception and sound transduction has also been investigated in several studies (Gauldie and Nelson, 1990; Popper and Lu, 2000; Schulz-Mirbach *et al.*, 2011; Inoue *et al.*, 2013). The conclusions suggest that bottom-dwelling fish have larger otoliths than pelagic species, which is a consequence of the development of their listening and communication capacity (greater than that of their vision capacity). These characteristics of otolith shape and size are also thought to be a consequence of their role in swimming, through the vestibular function, as fish with very fast swimming abilities and high acceleration rates have very small otoliths (Lychakov and Rebane, 2005).

Principal component analysis using individual data grouped by morphotype (round and flat fish) or by habitat (pelagic, demersal and benthic species) for the 22 main species in the Channel and North Sea shows that morphotypes or different habitats discriminate well between the 3D shape of otoliths (Figures 58 and 59). The otoliths of flatfish can be distinguished relatively well from those of roundfish (Figure 58). Similarly, depending on the environment (pelagic, demersal or benthic) in which the fish live, their functional adaptation has a particular influence on the shape of their otolith (Figure 59). It should be noted that there is no overlap between the six species of demersal fishes belonging essentially to the gadidae family (cod, whiting, haddock, pouting, seabass and sturgeon). So, although there is an evolution over the life of the fish (variation in the size of the otoliths), the 3D shape of the otoliths of these species is very specific, allowing good species recognition.

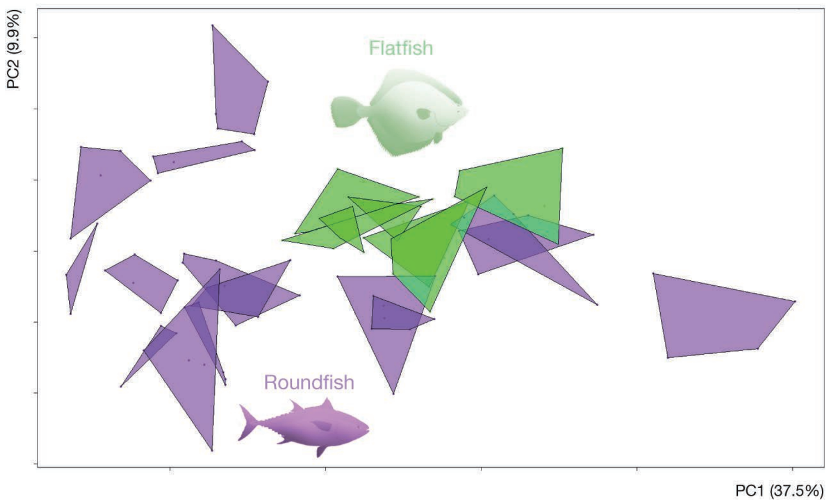


Figure 58. Graphical representation of the principal components PC1 and PC2 of the differences between the 3D shape of the otoliths of round and flat fish species.

Each species is represented by a coloured polygon and each point corresponds to an individual of the species analysed.

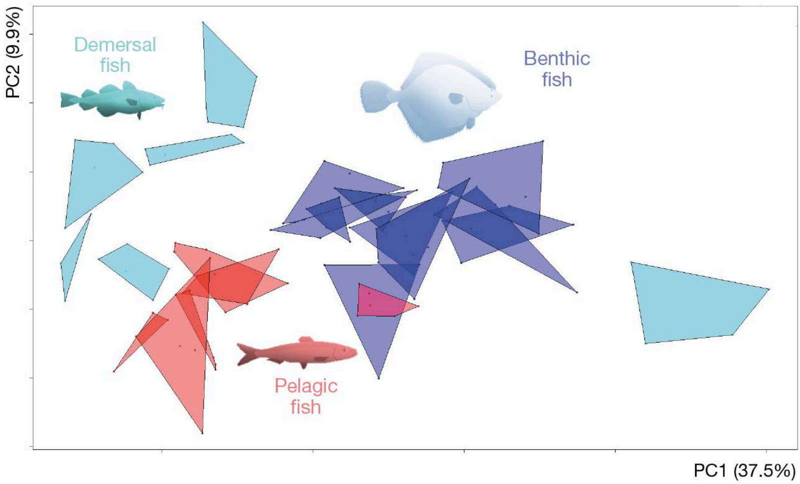


Figure 59. Graphical representation of the principal components PC1 and PC2 of the differences between the 3D shape of the otoliths of pelagic, demersal and benthic fish species.

Each species is represented by a coloured polygon and each dot corresponds to an individual of the species analysed.

Conclusions

Although the number of species covered in this identification guide is relatively small compared with previous works, it is highly innovative for four main reasons:

– this is the first time that a book has presented analyses of the shape of otoliths in 3D and not simply in 2D;

– for each species, the relationships between otolith shape parameters and fish size across the species size gradient are presented;

– graphical statistical analyses help users differentiate between species and identify those that may be confused with one another;

– 3D analyses show that species morphotypes (roundfish *versus* flatfish) or habitats (pelagic, demersal and benthic) discriminate well between otolith shapes.

Finally, this book clearly shows the benefits of using 3D images rather than simple 2D images, which are not always sufficiently representative of the overall shape.

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Appendix. Image acquisition parameters for each fish species

Nominal resolution in micrometres and aluminium filter size used for each fish species analysed.

Species common name	Nominal resolution in micrometres	Aluminium filter in millimetres
European anchovy	10	0.5
European seabass	13 to 18	0.5
Brill	10	0.5
Atlantic horse mackerel	10 to 15	0.5
Haddock	10 to 23	0.5 and 1
European flounder	10	0.5
Tub gurnard	10	0.5
Red gurnard	10	0.5
Atlantic herring	10	0.5
Common dab	10	0.5
Lemon sole	10	0.5
Atlantic mackerel	10	0.5
Whiting	10 to 24	0.5
Atlantic cod	10 to 18	1
European plaice	10	0.5
Striped red mullet	10	0.5
John Dory	10	0.5
European pilchard	10	0.5
Common sole	10	0.5
Sprat	10	0.5
Pouting	10 to 12	1
Turbot	10 to 12	0.5 and 1

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The otolith, a calcified structure in the inner ear of fish, evolves throughout the life of an individual and is generally used to estimate the age of the fish. So how do we analyze this tiny mineral particle, and what does it tell us about each species of fish?

This book provides a description and three-dimensional (3D) analysis of the otolith shapes of the main commercial fish species in the English Channel and North Sea.

This innovative approach, facilitated by the use of an X-ray microtomograph, makes it possible to specify otolith characteristics, differentiate fish populations and to locate them geographically.

Flatfish such as sole, dab, plaice and turbot, and roundfish from herring to haddock and gurnard: for each species, five individuals representative of the size range sampled in the marine environment were selected and their otolith shape described.

This guide is an invaluable resource for fisheries science, offering researchers, professionals and technicians a new way of refining their knowledge of Channel and North Sea species and individuals.

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