Oceanological and Hydrobiological Studies

International Journal of Oceanography and Hydrobiology

Volume 48, No. 3, September 2019
pages (296-304)

ISSN 1730-413X
eISSN 1897-3191

Shapes of otoliths in some Baltic fish and their proportions

by

Mariusz R. Sapota*, Violetta Dąbrowska

DOI: **10.2478/ohs-2019-0027**
Category: **Short communication**
Received: **November 06, 2018**
Accepted: **March 15, 2019**

University of Gdańsk, Faculty of Oceanography and Geography, Institute of Oceanography, Department of Marine Biology and Ecology, Al. M. Piłsudskiego 46, 81-378 Gdynia, Poland

* Corresponding author: *mariusz.sapota@ug.edu.pl*

Abstract

Otoliths are bony structures inside the fish labyrinth. They are used to determine the age of fish and to identify species based on their remains. The objective of this study was to describe the shape of otoliths in adult European perch (*Perca fluviatilis*), Atlantic herring (*Clupea harengus*), European sprat (*Sprattus sprattus*), lesser sand eel (*Ammodytes tobianus*), great sand eel (*Hyperoplus lanceolatus*), round goby (*Neogobius melanostomus*), European whitefish (*Coregonus lavaretus*), Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), European eel (*Anguilla anguilla*), viviparous eelpout (*Zoarces viviparus*), turbot (*Scophthalmus maximus*), European flounder (*Platichthys flesus*), European plaice (*Pleuronectes platessa*) and European smelt (*Osmerus eperlanus*). Fish were caught in the Gulf of Gdańsk. The relationships between the size of otoliths and the length of fish were established for adult European perch, European flounder, Atlantic herring and round goby. Otoliths of taxonomically related species were similar. It was not possible to differentiate otoliths of Ammodytidae, Pleuronectidae, Scophthalamidae, Anguilidae by comparing the presented results with the literature data. Otoliths of Zoarcidae, Osmeridae, Clupeidae, Gadidae, Gobiidae, Percidae and Salmonidae were quite similar but distinguishable. In most of the investigated species, otoliths grow proportionally to the fish size. Their shape does not change during the fish life. The shape of otoliths in the round goby changes significantly. Otoliths of small fish are rounded and significantly lengthen during the growth of fish.

Key words: otolith size, otolith shape, fish size

DE GRUYTER

The *Oceanological and Hydrobiological Studies* is online at www.oandhs.pl

Introduction

Otoliths are calcareous structures inside the labyrinth organ of the teleosts. They perform an acoustic and equilibrium function. Calcium carbonate is deposited in the sacculus, lagena and utriculus. Otoliths are good markers. In many cases, they allow the taxonomical identification of fish from skeletal remains. Their shape and size are related to fish taxonomy and life strategy. The differences between these calcareous structures can be used, inter alia, to study the taxonomy of extinct species and trophic preferences of predators. The largest otoliths (sagittae) may be helpful in estimating the total length of prey. Characteristic shapes and their variability may be helpful in fish taxonomy (Jobling & Breiby 1986; Tusset et al. 2006). The amount of otoliths in the stomach can be used to estimate the amount of ingested fish (Tollit et al. 1997).

Otoliths can be well preserved in fish fossils and allow taxonomic identification of extinct species. For example, the shape of otoliths found in *Lepidocottus aries* fossils indicates the affinity with the still existing Gobiidae family (Gierl et al. 2013).

The total length of fish (TL) can be estimated from the size of sagittae. Otoliths can also be used for assessing the seasonal variation in food preferences of predators, which in turn allows the construction of a food web model and the determination of the relative importance of individual fish taxa in the diet of different predators (Joyce et al. 2002; Phillips et al. 2001; Olsson & North 1997).

The important fact to consider is that otoliths isolated from stomachs or feces of predators are often dissolved and their parameters differ from those of undigested otoliths. The estimated number of ingested fish based on the number of otoliths may be incorrect due to the possible total dissolution of otoliths in the stomachs of predators (Bowen 2000; Jobling & Breiby 1986; Tollit et al. 1997).

The main objective of the presented research was to compare various shapes of sagittae recovered from adult fish of 17 species. Another objective was to define how the length and width of otoliths as well as the ratio of their length to width in adult European perch (TL from 12.5 to 21.0 cm), European flounder (TL from 8.8 to 26.0 cm), Atlantic herring (TL from 12.5 to 29.0 cm) and round goby (TL from 7.1 to 20.0 cm) are correlated with the total length of fish. For many fish species there are no equations that can be used to estimate the total length of fish based on parameters of otoliths (AFORO). For this reason, the research presented in this paper has been carried out, focusing on certain fish species from the Baltic Sea.

Materials and methods

Fish were collected in the Gulf of Gdańsk in 2011 and 2013 using gill nets. Otoliths were removed from the skulls of fish, cleaned from the remains of tissues and stored in paper envelopes. The species name and total length (TL) of each organism were provided on the envelopes.

Otoliths were immersed in ethanol and observed using a 0.75 zoom lens in the light reflected from the object. A stereoscopic microscope SMZ 18 Nikon was used for the observations. Photographs were taken by the Opta-Tech camera, supported by the OptaView-IS software. Digital pictures of otoliths were processed using GIMP 2.8.P and measured using Digimizer 4.6.1. The images were scaled using a known segment length in pixels.

The analysis of variation in the shapes of sagittae was conducted on adult fish representing the following species: European perch (*Perca fluviatilis*), Atlantic herring (*Clupea harengus*), European sprat (*Sprattus sprattus*), lesser sand eel (*Ammodytes tobianus*), great sand eel (*Hyperoplus lanceolatus*), round goby (*Neogobius melanostomus*), European whitefish (*Coregonus lavaretus*), Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), European eel (*Anguilla anguilla*), viviparous eelpout (*Zoarces viviparus*), turbot (*Scophthalmus maximus*), European flounder (*Platichthys flesus*), European plaice (*Pleuronectes platessa*) and European smelt (*Osmerus eperlanus*). The correlation between the length of otoliths, their width, the length/width ratio, the total length of fish, and changes in the shape of otoliths during the growth of fish was analyzed for European perch (TL ranged from 12.5 to 21.0 cm), European flounder (TL ranged from 8.8 to 26.0 cm), Atlantic herring (TL ranged from 12.5 to 29.0 cm) and round goby (TL ranged from 7.1 to 20.0 cm). Measurements of otoliths were transferred to the Libre Office calculation sheet. The length/width ratio of sagittae was calculated by dividing the length of otoliths by their width. The calculations and diagrams were made in the Libre Office calculation spreadsheet. The fish TL was expressed in cm and the length and width of otoliths in mm. For practical reasons (possibility of calculating the fish size based on the size of otoliths), we assumed that the fish TL depends on otolith measurements.

Results

The shape of otoliths varies from species to species. In the round goby, it changes during the growth of fish from an almost round one (Fig. 1a) to a very

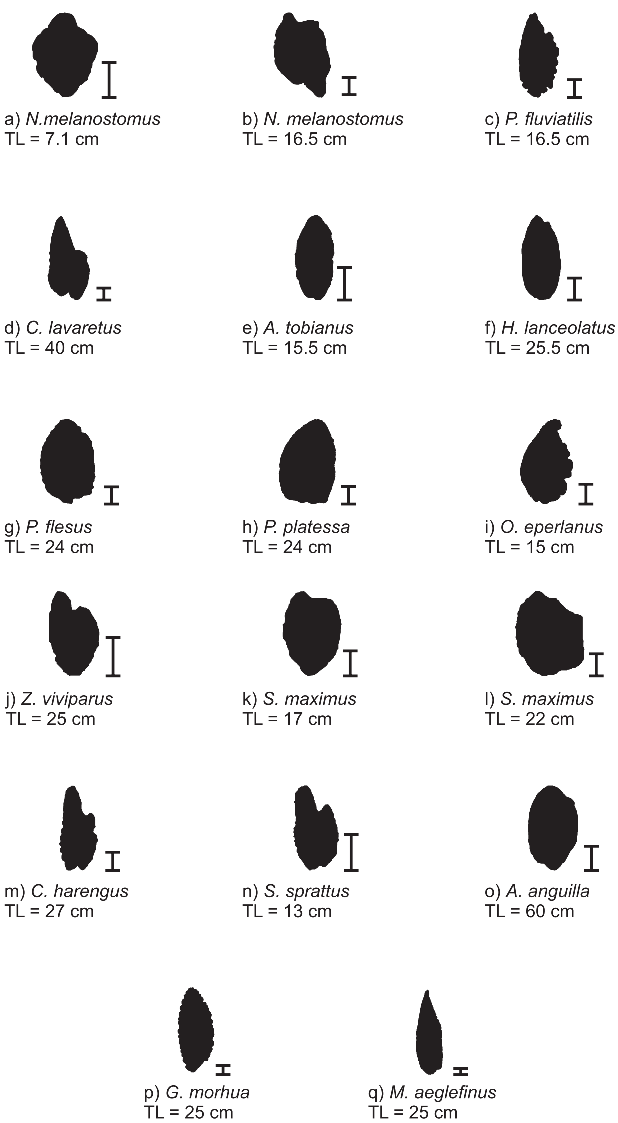

Figure 1

Shapes of otoliths extracted from selected Baltic fish species; vertical bars next to each otolith represent 1 mm length

characteristic shape (Fig. 1b), clearly different from the shapes of otoliths in other species examined during this research. Sagittae of the European perch are elliptical in shape with a sidelong cut, wavy margins and a short rostrum (Fig. 1c). Otoliths of the European whitefish (Fig. 1d) have an elliptical shape with smooth edges and an elongated, sharpened rostrum. The lesser sand eel (Fig. 1e) and the great sand eel (Fig. 1f) have elliptical sagittae with smooth margins. Otoliths of the European flounder (Fig. 1g) and the European plaice (Fig. 1h) bulge on one side and have wavy edges. Sagittae of the European smelt have a droplet shape with wavy edges (Fig. 1i). The shape of otoliths in viviparous eelpout is elliptical with an elongated, rounded rostrum (Fig. 1j). Otoliths of the turbot have an oval shape (Fig. 1k), which changes to a muffin shape (Fig. 1l) as the fish grows. Sagittae of the Atlantic herring (Fig. 1m) or the European sprat (Fig. 1n) have an elliptical shape with an elongated rounded rostrum. Otoliths of the Atlantic herring have wavy edges, while margins of otoliths in the European sprat are smooth. Oval-shaped otoliths were extracted from the European eel (Fig. 1o). Otoliths of the Atlantic cod have an elliptical shape and wavy edges (Fig. 1p), while otoliths of another Gadidae fish, i.e. haddock, are elongated with a sharpened postrostrum (Fig. 1q).

The TL of the investigated round goby individuals ranged from 7.1 to 20.0 cm. A round otolith was extracted from a specimen with a TL of 7.1 cm, whereas an otolith belonging to a specimen with a TL of 17.0 cm was more elongated. The relationship between the length of otoliths and the fish TL is described by the following equation: $y = 3.769x - 1.570$ (1) (Fig. 2a; Table 1). The equation describing the relationship between the total length of the fish and the width of otoliths takes the form of $y = 7.725x - 6.028$ (2) (Fig. 2b; Table 1). The increase in the length of sagittae in the round goby is greater than the increase in the width of otoliths (Fig. 2c; Table 1). The shape of otoliths changed from elliptical to elongated along the rostrum/postrostrum axis (Fig. 2d).

The TL of individuals of the European perch ranged from 12.5 to 21.0 cm. The function describing the relation between the TL of the European perch and

Table 1

Relations between otolith length, otolith width, otolith the length/width ratio and fish total length

species	n	total length (cm)		otolith length (mm)		otolith width (mm)		otolith length/width ratio	
		min.	max	equation	r	equation	r	equation	r
N. melanostomus	30	7.1	20.0	y = 3.769x – 1.570	0.988	y = 7.725x – 6.028	0.974	y = 25.545x – 26.655	0.837
P. fluviatilis	12	12.5	21.0	y = 4.273x – 4.862	0.976	y = 7.890x – 1.588	0.976	y = 24.491x + 70.207	0.657
P. flesus	21	8.8	26.0	y = 5.575x – 4.040	0.971	y = 9.629x – 6.041	0.976	y = 19.699x – 13.877	0.347
C. harengus	16	12.5	29.0	y = 7.005x – 6.099	0.967	y = 17.131x – 9.899	0.917	y = 19.758x – 21.645	0.585

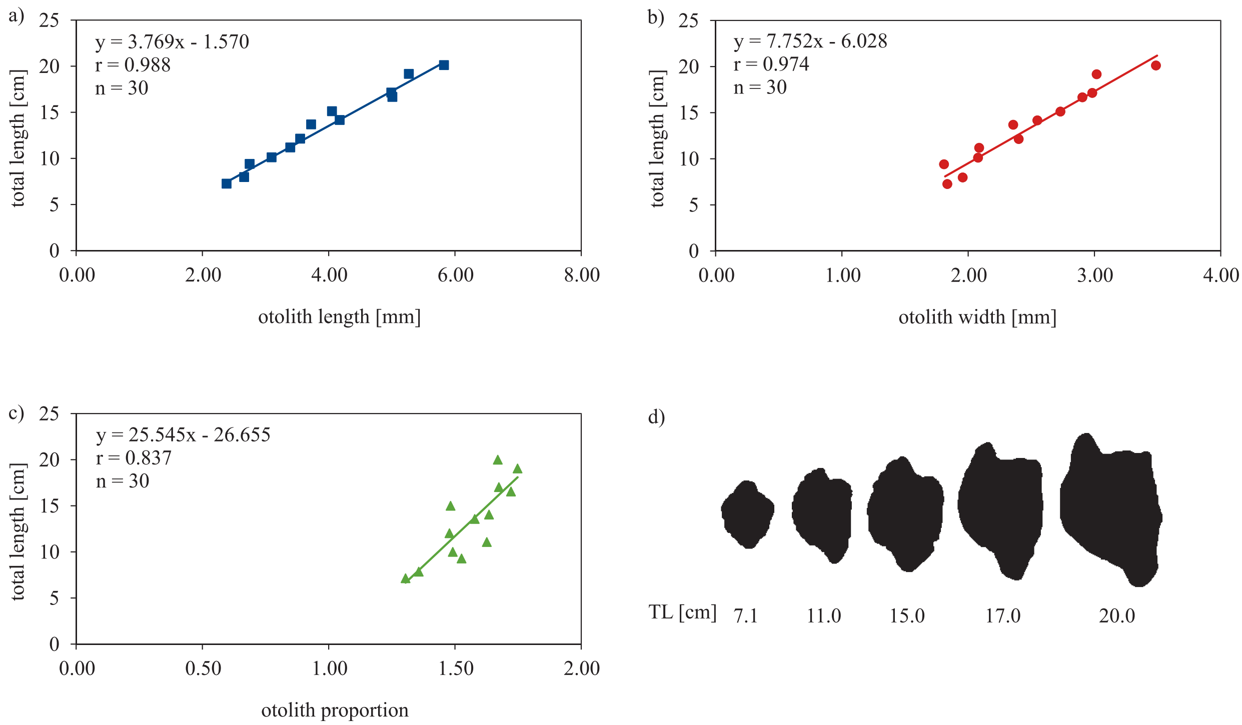

Figure 2

Relationship between TL of *N. melanostomus* and a) otolith length; b) otolith width; c) otolith length/width ratio; d) examples of otoliths

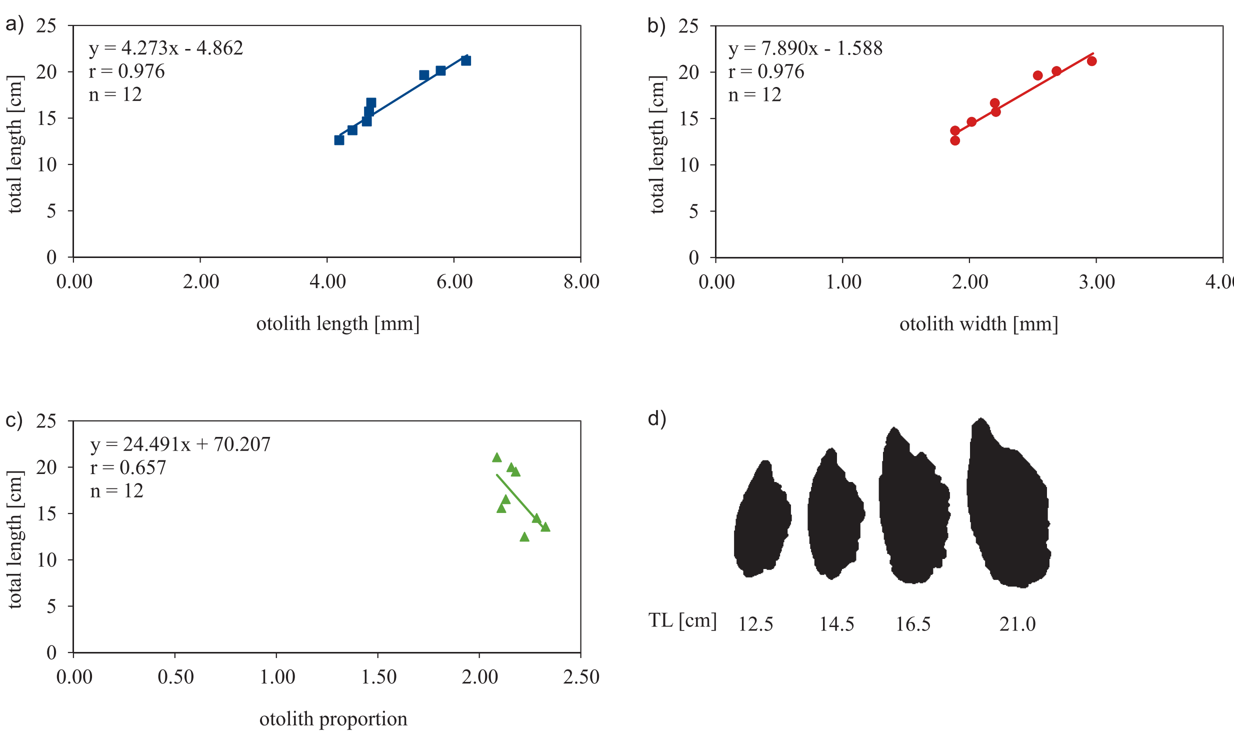

Figure 3

Relationship between TL of *P. fluviatilis* and a) otolith length; b) otolith width; c) otolith length/width ratio; d) examples of otoliths

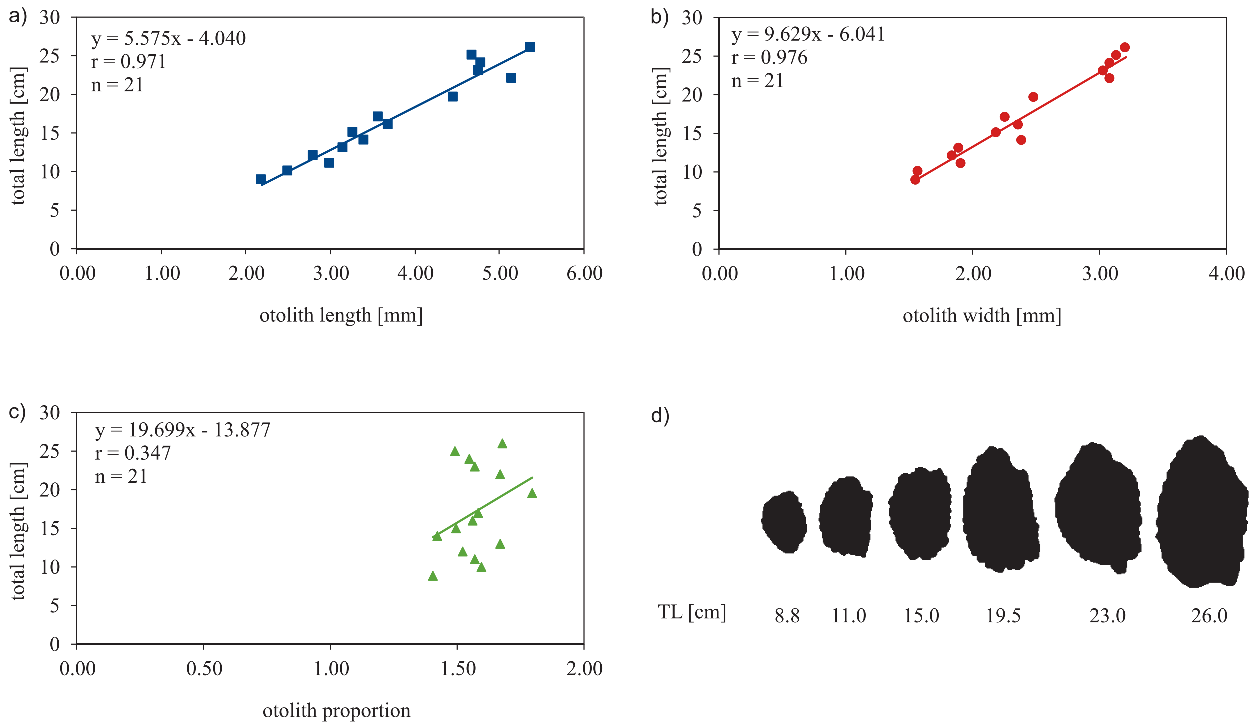

Figure 4

Relationship between TL of *P. flesus* and a) otolith length; b) otolith width; c) otolith length/width ratio; d) examples of otoliths

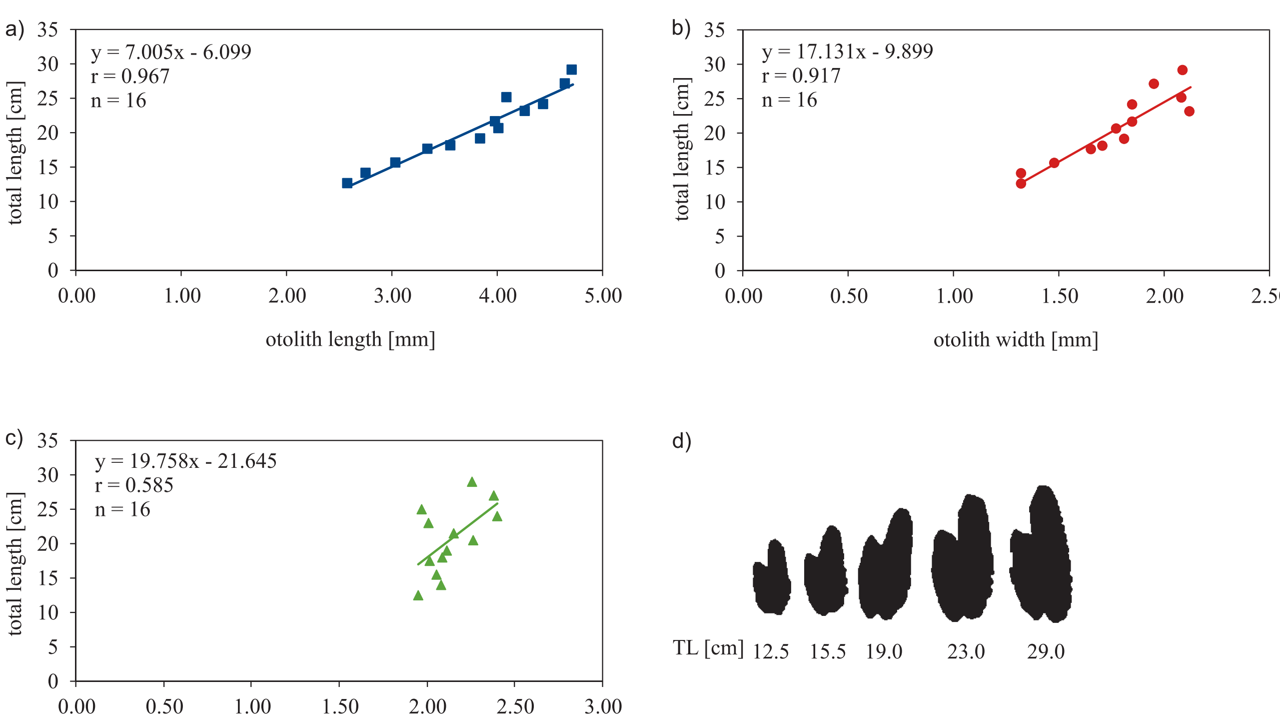

Figure 5

Relationship between TL of *C. harengus* and a) otolith length; b) otolith width; c) otolith length/width ratio; d) examples of otoliths the length of otoliths is y = 4.273x – 4.862 (3) (Fig. 3a; Table 1) and the relationship between the fish TL and the width of otoliths is y = 7.890x – 1.588 (4) (Fig. 3b; Table 1). The length of sagittae in the European perch increases at a slower rate than the width of otoliths (Fig. 3c; Table 1). The shape of otoliths is stable during the growth of fish (Fig. 3d).

The TL of the examined individuals of the European flounder ranged from 8.8 to 26.0 cm. The linear regression describing the relationship between the TL of the European flounder and the length of otoliths takes the following form: y = 5.575x – 4.040 (5) (Fig. 4a; Table 1). The function y = 9.629x – 6.041 (6) describes the relationship between the fish TL and the width of otoliths (Fig. 4b; Table 1). The length/width ratio of sagittae in the European flounder is stable during the fish growth and the length and width of otoliths increase proportionally (Fig. 4c; Table 1). The European flounder has elliptical otoliths. Their shape does not change during the fish growth (Fig. 4d).

The TL of the measured individuals of the Atlantic herring ranged from 12.5 to 29.0 cm. The shape of their otoliths does not change during the growth of the fish. The relationship between the TL of the Atlantic herring and the length of otoliths is described by the equation: y = 7.005x – 6.099 (7) (Fig. 5a; Table 1). The relationship between the fish TL and the width of otoliths is described by the equation y = 17.131x – 9.899 (8) (Fig. 5b; Table 1). Sagittae of the Atlantic herring grow faster in length than in width (Fig. 5c; Table 1). The general shape of otoliths in the Atlantic herring does not change during the fish growth (Fig. 5d).

Discussion

As evidenced by other authors, taxonomic identification of fish is possible based on the shapes of otoliths, but it is not as simple as it would seem. Some authors argue that otoliths are such a good marker that it is even possible to identify fish to the species level (Campana 2004; Jobling & Breiby 1986). Others, in turn, claim that sagittae of some fish are so similar to each other that only higher taxonomic units can be identified (Morrow 1979).

In the presented work, otoliths of taxonomically related species were similar. It was not possible to distinguish otoliths coming from the families: Ammodytidae, Pleuronectidae, Scophthalamidae, Anguilidae by comparing the presented results and the literature data, whereas otoliths of Clupeidae, Zoarcidae, Osmeridae, Gadidae, Gobiidae, Percidae, Salmonidae fish were quite similar but distinguishable. Otoliths in most of the examined species grow proportionally to the fish size and their shape does not change.

Descriptions of otoliths from various species and various geographical regions presented in the literature confirm the observations presented in this work.

The round goby with a TL of 7.1 cm has sagittae similar in shape to other small Gobiidae, like the sand goby (*Pomatoschistus minutus*) and the common goby (*P. microps*). When comparing the round goby with a TL of 15 cm and the black goby (*Gobius niger*) of the same length, we can see that their otoliths are slightly different. The rostrum and postrostrum of the black goby are bluntly terminated (AFORO) as opposed to those in the round goby, which are rounded.

Otoliths of the European perch and pikeperch (*Sander lucioperca*) have a similar shape (Poulet et al. 2004). However, otoliths of the European perch from Lake Ladik have an ellipsoidal shape (Ylmaz et al. 2014), which may be caused by different conditions prevailing in that habitat or may be genetically determined (Poulet et al. 2004).

When comparing the otoliths of the European whitefish and other Salmonidae, it can be observed that sagittae of various species differ from each other. Otoliths of the Atlantic salmon (*Salmo salar*) and the brown trout (*S. trutta*) have a more rounded and putted forward rostrum (Campana 2004) compared to otoliths of the whitefish. It is worth mentioning that research conducted on otoliths of the Atlantic salmon indicates that it is not possible to differentiate between fish populations based solely on the shape of otoliths (Friedlnad & Reddin 1994).

Fish from the Ammodytidae family have elliptical otoliths with smooth edges. This shape of otoliths is observed in the lesser sand eel and the great sand eel. The shape of otoliths in sand eels from the UK waters (Reay 1972) is the same as in fish from the Gulf of Gdańsk despite different environmental conditions.

Otoliths of the European flounder and the European plaice are bulged on one side and have wavy edges. Another plaice species, the American plaice (*Hippoglossoides platessoides*) and the common dab (*Limanda limanda*) have otoliths of a similar shape (AFORO).

Sagittae of the European smelt and the rainbow smelt *O. mordax* (Campana 2004) are droplet-shaped with wavy edges, but the capelin (*Mallotus vilosus*) living in the North Atlantic waters has otoliths of a different shape, despite their close taxonomic affinity (Campana 2004).

Otoliths of the Zoarcidae family differ in shape within each species. Sagittae of the viviparous eelpout are elliptical with a short and rounded rostrum, while otoliths of the polar eelpout (*Lycodes polaris*) from the White Sea have a very specific shape, different from those of the viviparous eelpout from the Baltic Sea (Svetocheva et al. 2007).

Scophthalamidae fish have muffin-shaped otoliths. For example, otoliths of the brill (*S. rhombus*) are very similar to those of the turbot (AFORO).

Otoliths of the Atlantic herring and the European sprat are very similar but distinguishable. Both shapes are elliptical with wavy edges and an elongated, rounded rostrum, but otoliths of the European sprat are wider than those of the Atlantic herring. The Atlantic herring from the Celtic Sea and the Irish Sea has otoliths of the same shape as those from the Baltic Sea described above. The only difference observed was the length of sagittae. This can be used to indicate which population the fish belong to (Burke et al. 2008). Sagittae of the allis shad (*Alosa alosa*) and twait shad (*A. fallax*) are very similar in shape (AFORO).

When comparing the European eel from the Baltic Sea and the Mediterranean Sea, it appears that despite different habitats, the otoliths of these fish are of the same shape. However, Fourier analysis revealed differences between the compared otoliths. It can be indicated as a marker of the environmental impact, especially salinity, on the growth and shape of otoliths (Capoccioni et al. 2011).

Sagittae of haddock (*Melanogrammus aeglefinus*) and whiting (*Merlangius merlangus*) are elongated with a sharp postrostrum (AFORO). They differ from otoliths of the Atlantic cod, which are elliptical with wavy edges. Otoliths of the Atlantic cod from waters near the Faroe Islands were slightly different in shape, which may be due to genetic differences as well as environmental factors (Cardinale et al. 2004).

When comparing the collected otoliths with photographs available on the AFORO website and in the literature, it has been confirmed that in many cases it is possible to determine higher taxonomic units (Morrow 1979). In some cases, the variability in the shape of sagittae allows the identification of a species or a population of fish. Some studies have shown that different shapes of otoliths within a family, genus or between populations of the same species can be observed using the Fourier description (Bird et al. 1986; Burke et al. 2008; Galley et al. 2006). Details can be easily omitted without harmonic shape analysis. The observed differences are mainly due to the genetic variance between taxa or populations as well as the impact of environmental conditions (Campana & Casselman 1993; Poulet et al. 2004). These factors have a crucial impact on the growth of fish and consequently on the growth and shape of otoliths (Cardinale et al. 2004; Campana & Casselman 1993). The identification of fish taxa should not be based solely on the shape of sagittae, but all parameters of otoliths should be examined such as length, width and surface area (Burke et al. 2008; Turan 2000). It is also difficult to identify fish taxa when fish are young (Campana & Casselman 1993). As mentioned above, in some cases, the shape of sagittae may change during the growth of fish. It is worth noting that during the process of digestion many characteristic features of otoliths can be dissolved and the identification of taxa would be impossible (Jobling & Breiby 1986; Morrow 1979).

Estimation of the fish TL based on parameters of otoliths is yet another scientific application of otoliths. Within the investigated fish TL range, a clear correlation between the parameters of otoliths and the fish TL enables the estimation of the fish TL based on parameters of otoliths. Parameters of otoliths could be useful for estimating the size of fish ingested by a mammal, bird or another fish, but otoliths from stomachs or feces are often dissolved. Their length and width may be reduced, which leads to an underestimation of the fish TL (Jobling & Breiby 1986; Tollit et al. 1997). The size of sagittae may vary in fish of the same size within the same species, which may indicate differences in habitats occupied by fish. Research has shown that some fish living at greater depths, have larger otoliths than specimens of the same species living in shallower water. This phenomenon results from the fact that larger otoliths are more effective in reception of sound waves and play a crucial role at greater depths where hearing is more important (Paxton 2000; Cruz & Lombarte 2004). Temperature is the main factor affecting the fish growth. Higher temperature intensifies the growth of fish and consequently the growth of otoliths (Folkvord et al. 2004; Mosegaard et al. 1988). This may be one of the reasons why fish of the same species and size may have otoliths of slightly different sizes (Merigot et al. 2007). The AFORO website provides many equations, which allow us to estimate the fish TL based on the length of otoliths, but there are no equations for the species examined in this work. The described relationships may vary between areas (Bostanci 2009), so it is important to apply them to fish living in the Gulf of Gdańsk.

There are three models of the growth of otoliths. The first model is based on a faster increase in the length of otoliths compared to their width. This relationship is observed for the round goby and Atlantic herring. The second model assumes a faster increase in the width of otoliths compared to their length. It is observed in the case of the European perch. The third model is based on an isometric increase in the length and width of otoliths during the lifespan of fish. The third model is typical for the European flounder.

The shape of otoliths may change during the life of fish, but this is not always the case. In the examined range of the fish TL, it was observed that the shape of otoliths does not change for the European perch, European flounder and Atlantic herring. On the other hand, the shape of otoliths of the round goby changes significantly during the life of the fish. There is a significant difference in the case of individuals with a TL of 11 cm, where the round sagitta changes into a more elongated shape, which is very specific to this species. Probably a similar situation can be observed for the turbot, but due to the narrow range of TL in the examined material and the small number of fish, further research is still needed. The change in the shape of otoliths is a genetically determined characteristic for a given species. Environmental conditions are the second cause that may be associated with the variations in the shape of otoliths (Vignon 2012). Changes in the shape of sagittae during the fish growth may cause a taxonomic misidentification of larvae or juvenile forms at the species level (Jobling & Breiby 1986) if based only on their otoliths. In many cases, the correct taxonomic identification of fish is not possible without the knowledge of how the shape of otoliths changes during the life of fish.

References

Bird, J.L., Eppler, D.T. & Checkley Jr, D.M. (1986). Comparisons of herring otoliths using Fourier series shape analysis. *Canadian Journal of Fisheries and Aquatic Sciences* 43(6): 1228–1234. DOI: 10.1139/f86-152.

Bostanci, D. (2009). Otolith biometry-body length relationships in four fish species (chub, pikeperch, crucian carp, and common carp). *Journal of Freshwater Ecology* 24(4): 619–624. DOI: 10.1080/02705060.2009.9664339.

Bowen, W.D. (2000). Reconstruction of pinniped diets: accounting for complete digestion of otoliths and cephalopod beaks. *Canadian Journal of Fisheries and Aquatic Sciences* 57(5): 898–905. DOI: 10.1139/f00-032.

Burke, N., Brophy, D. & King, P.A. (2008). Shape analysis of otolith annuli in Atlantic herring (Clupea harengus); a new method for tracking fish populations. *Fisheries Research* 91(2–3): 133–143. DOI: 10.1016/j.fishres.2007.11.013.

Campana, S.E. (2004). *Photographic Atlas of Fish Otoliths of the Northwest Atlantic Ocean*. Ottawa, Ontario: NRC Research Press.

Campana, S.E. & Casselman, J.M. (1993). Stock discrimination using otolith shape analysis. *Canadian Journal of Fisheries and Aquatic Sciences* 50(5): 1062–1083. DOI: 10.1139/f93-123.

Capoccioni, F., Costa, C., Aguzzi, J., Menesatti, P. & Lombarte, A. (2011). Ontogenetic and environmental effects on otolith shape variability in three Mediterranean European eel (*Anguilla anguilla*, L.) local stocks. *Journal of Experimental Marine Biology and Ecology* 397(1): 1–7. DOI: 10.1016/j.jembe.2010.11.011.

Cardinale, M., Doering-Arjes, P., Kastowsky, M. & Mosegaard, H. (2004). Effects of sex, stock, and environment on the shape of known-age Atlantic cod (*Gadus morhua*) otoliths. *Canadian Journal of Fisheries and Aquatic Sciences* 61(2): 158–167. DOI: 10.1139/f03-151.

Cruz, A. & Lombarte, A. (2004). Otolith size and its relationship with colour patterns and sound production. *Journal of Fish Biology* 65(6): 1512–1525. DOI: 10.1111/j.0022-1112.2004.00558.x.

Folkvord, A., Johannessen, A. & Moksness, E. (2004). Temperature-dependent otolith growth in Norwegian spring-spawning herring (*Clupea harengus* L.) larvae. *Sarsia* 89(5): 297–310. DOI: 10.1080/00364820410002532.

Friedland, K.D. & Reddin, D.G. (1994). Use of otolith morphology in stock discriminations of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* 51(1): 91–98. DOI: 10.1139/f94-011.

Galley, E.A., Wright, P.J. & Gibb, F.M. (2006). Combined methods of otolith shape analysis improve identification of spawning areas of Atlantic cod. *ICES Journal of Marine Science*. 63(9): 1710–1717. DOI: 10.1016/j.icesjms.2006.06.014.

Gierl, C., Reichenbacher, B., Gaudant, J., Erpenbeck, D. & Pharisat, A. (2013). An extraordinary gobioid fish fossil from southern France. *PloS one* 8(5): e64117. DOI: 10.1371/journal.pone.0064117.

ICM, CSIC, UPC, UVIC. (2017, November). *Shape Analysis of Fish Otoliths*. Retrived February 16, 2018, from http://isis.cmima.csic.es/aforo/startDB_en.jsp.

Jobling, M. & Breiby, A. (1986). The use and abuse of fish otoliths in studies of feeding habits of marine piscivores. *Sarsia* 71(3–4): 265–274. DOI: 10.1080/00364827.1986.10419696.

Joyce, W.N., Campana, S.E., Natanson, L.J., Kohler, N.E., Pratt Jr, H.L. et al. (2002). Analysis of stomach contents of the porbeagle shark (*Lamna nasus* Bonnaterre) in the northwest Atlantic. *ICES Journal of Marine Science* 59(6): 1263–1269. DOI: 10.1006/jmsc.2002.1286.

Merigot, B., Letourneur, Y. & Lecomte-Finiger, R. (2007). Characterization of local populations of the common sole *Solea solea* (Pisces, Soleidae) in the NW Mediterranean through otolith morphometrics and shape analysis. *Marine Biology* 151(3): 997–1008. DOI: 10.1007/s00227-006-0549-0.

Morrow, J.E. (1979). *Preliminary keys to otoliths of some adult fishes of the Gulf of Alaska, Bering Sea, and Beaufort Sea*. Washington, DC: U.S. Department of Commerce, NOAA, NMFS. (NOAA Technical Report NMFS Circular, 420).

Mosegaard, H., Svedäng, H. & Taberman, K. (1988). Uncoupling of somatic and otolith growth rates in Arctic char (*Salvelinus alpinus*) as an effect of differences in temperature response. *Canadian Journal of Fisheries and Aquatic Sciences*. 45(9): 1514–1524. DOI: 10.1139/f88-180.

Olsson, O. & North, A. W. (1997). Diet of the king penguin Aptenodytes patagonicus during three summers at South Georgia. *Ibis* 139(3): 504–512. DOI: 10.1111/j.1474-919X.1997.tb04666.x.

Paxton, J. R. (2000). Fish otoliths: do sizes correlate with taxonomic group, habitat and/or luminescence? *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 355(1401): 1299–1303. DOI: 10.1098/rstb.2000.0688.

Phillips, K.L., Jackson, G.D. & Nichols, P.D. (2001). Predation on myctophids by the squid *Moroteuthis ingens* around Macquarie and Heard Islands: stomach contents and fatty acid analyses. *Marine Ecology Progress Series* 215: 179–189. DOI: 10.3354/meps215179.

Pothin, K., Gonzalez-Salas, C., Chabanet, P. & Lecomte-Finiger, R. (2006). Distinction between Mulloidichthys flavolineatus juveniles from Reunion Island and Mauritius Island (south-west Indian Ocean) based on otolith morphometrics. *Journal of Fish Biology* 69(1): 38–53. DOI: 10.1111/j.1095-8649.2006.01047.x.

Poulet, N., Berrebi, P., Crivelli, A.J., Lek, S. & Argillier, C. (2004). Genetic and morphometric variations in the pikeperch (*Sander lucioperca* L.) of a fragmented delta. *Archiv für Hydrobiologie* 159(4): 531–554. DOI: 10.1127/0003-9136/2004/0159-0531.

Reay, P.J. (1972). The Seasonal Pattern of Otolith Growth and its Application to Back-Calculation Studies in *Ammodytes tobianus* L. *ICES Journal of Marine Science* 34(3): 485–504. DOI: 10.1093/icesjms/34.3.485.

Svetocheva, O., Stasenkova, N. & Fooks, G. (2007). *Guide to the otoliths of the bony fishes of the White Sea*. Arkhangelsk: IMR/PINRO Joint Report Series No. 3/2007.

Tollit, D.J., Steward, M.J., Thompson, P.M., Pierce, G.J. & Santos, M.B. (1997). Species and size differences in the digestion of otoliths and beaks: implications for estimates of pinniped diet composition. *Canadian Journal of Fisheries and Aquatic Sciences* 54(1): 105–119. DOI: 10.1139/f96-264.

Tracey, S.R., Lyle, J.M. & Duhamel, G. (2006). Application of elliptical Fourier analysis of otolith form as a tool for stock identification. *Fisheries Research* 77(2): 138–147. DOI: 10.1016/j.fishres.2005.10.013.

Turan, C. (2000). Otolith shape and meristic analysis of herring (*Clupea harengus*) in the North-East Atlantic. *Archive of Fishery and Marine Research* 48(3): 213–225.

Tuset, V.M., Rosin, P.L. & Lombarte, A. (2006). Sagittal otolith shape used in the identification of fishes of the genus Serranus. *Fisheries Research* 81(2): 316–325. DOI: 10.1016/j.fishres.2006.06.020.

Vignon, M. (2012). Ontogenetic trajectories of otolith shape during shift in habitat use: Interaction between otolith growth and environment. *Journal of Experimental Marine Biology and Ecology* 420: 26–32. DOI: 10.1016/j.jembe.2012.03.021.

Yilmaz, S., Yazicioglu, O., Saygin, S. & Polat, N. (2014). Relationships of otolith dimensions with body length of European perch, *Perca fluviatilis* L., 1758 from Lake Ladik, Turkey. *Pakistan Journal of Zoology* 46(5): 1231–1238.