FEATURE:
FISHERIES HISTORY

Earliest References to Age Determination of Fishes and Their Early Application to the Study of Fisheries

James R. Jackson
Jackson is senior research associate in the Department of Natural Resources at the Cornell University Biological Field Station, Bridgeport, New York. He can be contacted at jrj26@cornell.edu.

ABSTRACT: Age data are routinely used in fish population studies today. While various works have touched upon aspects of the history of fish aging techniques, there does not appear to be a single source that attempts to summarize the earliest literature on age determination of fishes in a broad historical context. The Fisheries Management Section formed the ad hoc Assessment of Fish Aging Techniques Committee in 2006, with development of such a review as a goal. The earliest references to rings on the hard structures of fish by Leeuwenhoek and Hederström date to the seventeenth and eighteenth centuries. Scientific validation of annuli on the scales of fish did not take place until the late 1800s, with the work of Hintze and Hoffbauer. The work of Reibisch on otoliths and Heincke with other hard structures quickly followed. These later studies on fish aging techniques came at a time when large-scale studies of fish populations were gaining momentum. While the new aging methods were adopted rapidly by many fisheries workers, debates about their validity were not uncommon. A notable example took place between Hjort and Thompson, centering on Thompson's doubts concerning the validity of scale-based ages in Hjort's seminal 1914 paper.

Referencias elementales para la determinación de edad en peces y sus primeras aplicaciones en el estudio de las pesquerías

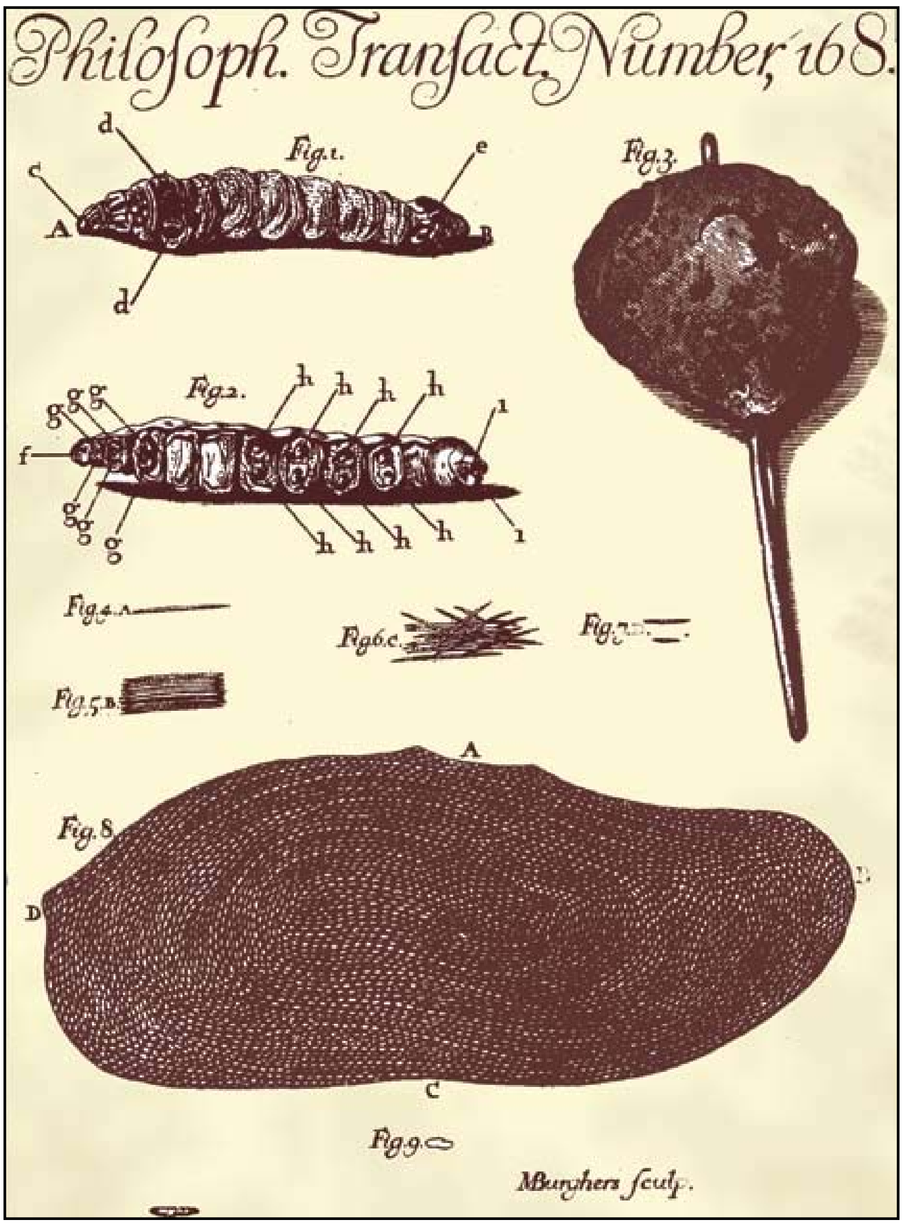
RESUMEN: En la actualidad, los datos de edad son comúnmente utilizados en estudios poblacionales de peces. Si bien existen varios trabajos que abordan aspectos relacionados a la historia de las técnicas para determinar la edad en peces, parece no haber una sola referencia en la que, bajo un contexto histórico, se sintetice la información de los primeros estudios sobre este tema. Para tal fin, en 2006, La Sección sobre Manejo de Pesquerías estableció el Comité para la Evaluación de Técnicas de Determinación de Edad en Peces. Las primeras referencias acerca de anillos de crecimientos en estructuras duras en peces, de Leeuwenhoek y Hederström, se remontan a los siglos XVII y XVIII. La validación científica de los anillos presentes en las escamas de los peces no se dio sino hasta finales de 1800, con el trabajo de Hintze y Hoffbauer, seguido por los estudios de Reibisch sobre otolitos y otras estructuras duras. Estos trabajos se dieron al mismo tiempo en el que los estudios a gran escala de biología poblacional de peces ganaban inercia. Mientras que los nuevos métodos para determinación de edad fueron rápidamente adoptados por varios estudiosos de las pesquerías, crecieron los debates acerca de su validez. Un ejemplo fue la controversia suscitada entre Hjort y Thompson, generada por las dudas de Thompson acerca de la validez de los datos de edad publicados en un artículo de Hjort en 1914, obtenidos a partir de la lectura de escamas.

The use of age information is an integral part of fisheries today. Hilborn and Walters (1992:167) state that "the most valuable information obtained from sampled catch, at least for temperate waters, is age." The development and acceptance of methods for age determination in fishes represents a critical early stage in fisheries science, and at times was fraught with more controversy than today's wide usage of the methods would suggest. In 2006, the Fisheries Management Section of the American Fisheries Society formed the ad hoc Assessment of Fish Aging Techniques Committee to assess the status of aging of freshwater fishes in North America (see Maceina et al. this issue). As part of the committee's goals, an historical survey of the earliest references to aging of fishes and their initial application to fisheries studies was undertaken. Earlier works on fish aging have touched on aspects of the history of the field, often focusing on specific structures or species (e.g., Van Oosten 1929; Menon 1950), but many of these works appear in outlets that are not easily accessible. I am not aware of a single source that attempts to summarize the earliest works on age determination in fishes in their historical context, including their acceptance and initial application to the study of fisheries in the early years of the 1900s. The objective of this article is to provide such a summary and serve as a reference for those wishing to access original sources. In most cases, primary source material has been used by the author, but in those cases where original documents were unavailable, original citations are still provided for historical purposes, with acknowledgement of the secondary source for the citation.

Aristotle (ca. 340 B.C.) may have been the first to speculate upon the use of hard structures to determine fish age, claiming in his *Historia Animalium* that "the age of a scaly fish may be told by the size and hardness of its scales" (Thompson 1910:Book

VIII, Section 30). However, it was not until the development of the microscope that more detailed studies of scale structure took place. Antoni van Leeuwenhoek of Holland, who used his experience counting threads in cloth at a dry goods store with magnifying glasses to develop improved lenses that he used to construct microscopes, became one of the leading microscopists of the 1600s. Leeuwenhoek possessed a wide-ranging curiosity that included issues surrounding demographics of animal populations (Egerton 1968). Curiously, Leeuwenhoek's studies of fish scales appear to have been at least in part inspired by Biblical strictures against eating fish without scales. His earliest writings on fish scales appeared in a letter to the Royal Society of London, and focused on the European eel (*Anguilla anguilla*) and the burbot (*Lota lota*), which he was drawn to as a result of their reported lack of scales "which two sorts of fish, the Jews will not eat, as forbidden by the Law of Moses." (Leeuwenhoek 1685:893). Leeuwenhoek found scales on both eel and burbot and undertook a study of the fine structure of eel scales, which included his observation of "circular lines" (Leeuwenhoek 1685:894; Figure 1). Leeuwenhoek observed that "altho [sic] all the scales, are not just of the same shape, I have yet observed, in many of them, as I judged, the same number of circular lines. From whence I conclude, that every year, the scale encreased [sic] one circular line..." (Leeuwenhoek 1685:894-895). A more detailed version of Leeuwenhoek's studies of fish scales, published in a volume of collected writings, included a description of the ring pattern on the scales of carp (*Cyprinus carpio*), as well as his speculation that the ring pattern resulted from the growth of new, larger scales underneath older scales. However, he nonetheless correctly inferred the timing of the formation of darker areas as occurring during the season of slowed growth, as he had previously observed in trees (Leeuwenhoek 1798).

Figure 1. The plate accompanying Leeuwenhoek's original theory that rings on the scale of eel were formed annually and could be used for determining age. Leeuwenhoek's illustration of scale patterns is presented as Fig.8, Fig. 9 shows an eel scale to scale (Leeuwenhoek 1685).



It seems that Leeuwenhoek's work went largely undiscovered by fisheries workers, as the attribution for the first reliable age determination more often is credited to Hans Hederström (e.g., Ricker 1975). Hederström, a Swedish clergyman, was drawn to his studies of fish aging by reports of a 267-year-old pike (*Esox lucius)* known as Heibrun's pike (Hederström 1759; Casselman 1974). Hederström asked, "Is it in agreement with the order established within the animal kingdom that nobler and more useful animals should have such a short span of life compared with that of the pike?" (Hederström 1759:161). Trusting that the Creator might provide some means of determining the age of fish, as was the case with trees, Hederström examined the vertebrae of pike and concluded that the rings that could be discerned on them were growth rings that could be used to determine the fish's age. His reasoning revealed a thoroughly scientific approach, and included verification that (1) both sides of a vertebra had the same number of rings, (2) all vertebrae in an individual possessed the same number of rings, (3) larger fish had more rings on their vertebrae than smaller fish, and (4) the number of rings matched the age of fish "known either from experience or from other circumstances" (Hederström 1759:162). Hederström went on to present length-at-age data for pike that agree well with modern estimates and also reported that he had confirmed the applicability of using rings on vertebrae for determining the age of a variety of other species, including European perch (*Perca fluviatilis*), roach (*Rutilus rutilus*), bream (*Abramis brama*), chub (*Leuciscus cephalus*), cod (*Gadus morhua*), European eel, and burbot.

While Hederström alluded to the use of known-age fish to verify his conclusions of annually-formed rings on fish vertebrae, fully-documented validations of the formation of annuli in the hard structures of fish did not appear in the literature until 100 years later. Robert Pell (1859) reported that his examination of the scales of yellow perch (*Perca flavescens*) and the vertebrae of sucker (*Catastomus* spp.) he had reared in ponds for two years exhibited two "rings or circles," and he concluded that the rings could be used to determine the age of all fish (Pell 1859:347). G. Hintze (1888, as cited and summarized in Van Oosten 1929) presented the results of his studies of the scales of known-aged carp from commercial ponds. Hintze presented illustrations of scales of age 1–4 carp, clearly showing addition of annuli, but with an erroneous interpretation of an accessory annuli in the age-2 fish that Van Oosten (1929) speculated may have lessened the impact of his work.

It was not until 1898, more than 200 years after Leeuwenhoek's original theories about the significance of patterns on fish scales, that the matter was finally subjected to thorough and critical study by C. Hoffbauer. Like Hintze, Hoffbauer studied carp from commercial ponds. His initial and most frequently cited paper was published in 1898, and was followed by more detailed studies in 1900 (Hoffbauer 1898 [Figure 2], 1900a; 1900b). Hoffbauer carefully observed the development of scales through the year, noting that during the season of growth, marginal, concentric rings were easily discernable and widely spaced, but as growth slowed and ultimately ceased during the winter they became more closely compacted, with a subsequent renewal of the pattern of widely-spaced circuli when growth resumed. He correctly concluded that the darker areas formed by closely-arranged circuli during the winter could be interpreted as representing annual marks and therefore used to age fish. Hoffbauer followed the formation of annuli on carp up to age 3, and then went on to examine the effects of environmental conditions on scale development. Among his findings were observations that scales from undernourished carp were characterized by less clearly defined and more closely arranged annuli. Further experimentation confirmed that spacing of annuli was correlated with the growth rate of fish, with fast growth resulting in more widely spaced annuli. Hoffbauer's later work included application of his new techniques to goldfish (*Carassius auratus*), largemouth bass (*Micropterus salmoides*), European perch, pike, and salmon (*Salmo* spp.). J. Stuart Thomson, with encouragement and support from Walter Garstang and E. J. Allen at the Plymouth Laboratory of the Marine Biological Association of the United Kingdom, extended Hoffbauer's work with freshwater fishes to important commercial marine species. His detailed work with pollack (*Pollachius pollachius*), poor cod (*Trisopterus minutus*), whiting (*Merlangius merlangius*), haddock (*Melanogrammus aeglefinus*), and cod convinced him that Hoffbauer's findings could be applied to marine species (Thomson 1902, 1904).

Investigations into the potential of structures other than scales for aging fish followed soon after Hoffbauer's publication. Johannes Reibisch, working with the Commission for the Scientific Investigation of German Seas at Kiel, quickly tried to apply Hoffbauer's findings in his studies of plaice (*Plueronectes platessa*), but was soon frustrated by the difficulty in accurately identifying annuli on scales. His experiences led him to look at another structure, and in 1899 he published the first paper on the utility of otoliths for determining the age of fish (Reibisch 1899, Figure 3).

Crowding of the rings in the otoliths of older plaice led Friedrich Heincke, also with the German Commission at Kiel, to examine the usefulness of a variety of fish bones for age determination. Working with gadids and flatfish, Heincke found annuli in the vertebrae, opercula, and several bones in the pectoral girdle (Heincke 1905, as cited and summarized in Menon 1950), and it is his work that is most often cited in conjunction with Hoffbauer and Reibisch as completing the early studies establishing scales, otoliths, and bones as viable aging structures (e.g., Allen 1917; Ricker 1975). Menon (1950) credits Tereschenko (1913), who was working with roach, with the first use of cleithra for aging and Holtzmayer (1924) with first using fin rays as part of his work with sturgeon (*Acipenser* spp.). So within 250 years

Figure 2. Illustration of annuli on the scales of carp from Hoffbauer (1898).

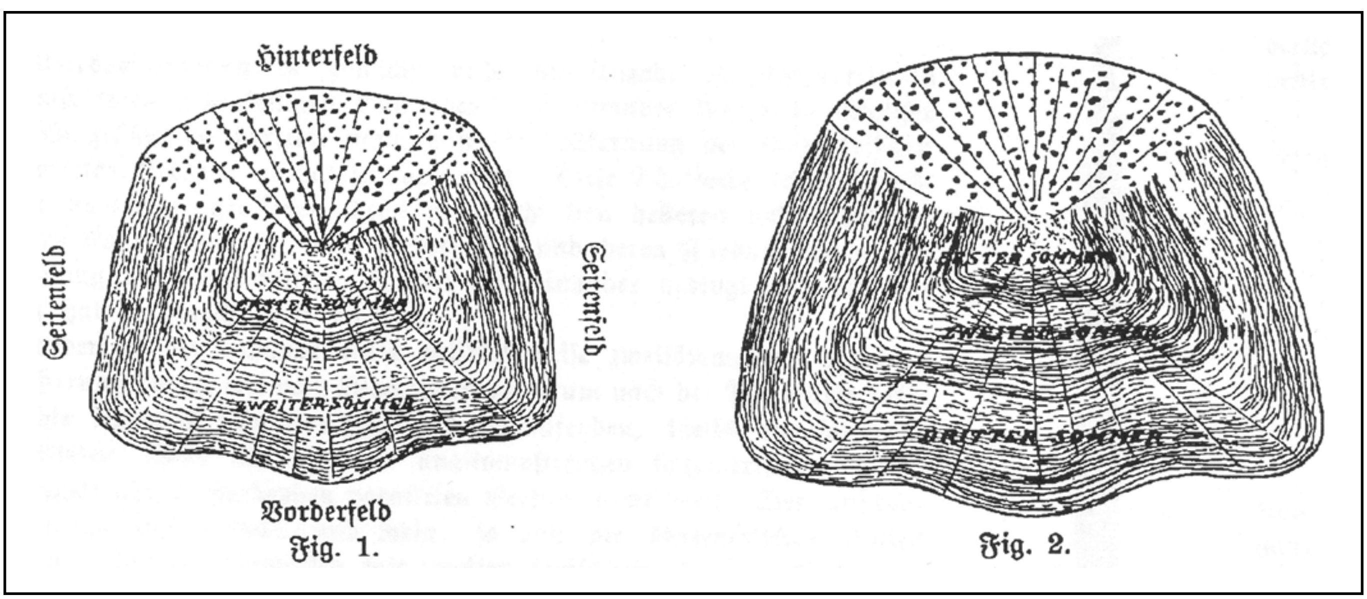
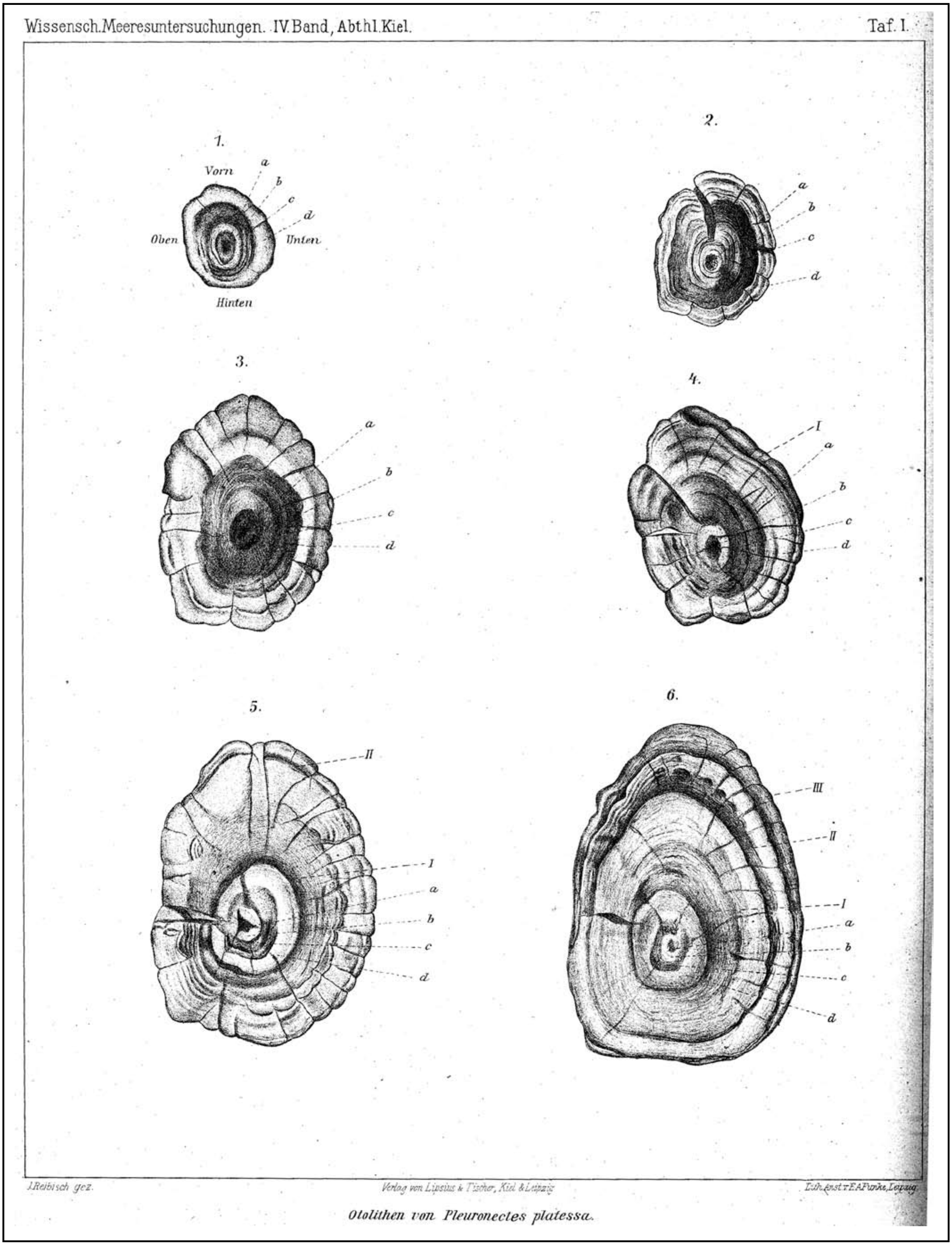


Figure 3. Plate illustrating annuli on otoliths of plaice (Reibisch 1899).



of Leeuwenhoek's first published observations of annuli on scales, those structures relied upon for the majority of aging of freshwater species in North America had been introduced to the literature (Maceina et al. this issue).

The findings of Hoffbauer and Reibisch could not have been better timed for notice and near-immediate application to the questions of fisheries. Fluctuations in the commercial catches of sea fishes had begun to attract serious attention in the later decades of the 1800s. Analyses of commercial catches and the initiation of large-scale fishery-independent surveys would soon take fisheries research in a direction where age-based data could lead to seminal breakthroughs that would change the way fish population dynamics were viewed.

Questions about age-specific processes would arise soon after systematic analyses of fisheries catches began. In the absence of wide-spread knowledge of the potential utility of hard structures for age determination, it is not surprising that early efforts at assigning ages to fish by fisheries workers were based on length information. While Carl Georg Johannes Petersen is most often credited with first proposing length-based methods for age determination (e.g., Allen 1917; Ricker 1975), his work appears to have been preceded by Joseph T. Cunningham. Cunningham, working at the Marine Biological Association's Plymouth Lab, attempted to use lengths from known-aged fish he reared in aquaria to assign ages to wild-caught fish, focusing on flatfish and cod (Cunningham 1891, 1892). Cunningham's efforts were not rewarded by clear-cut results: "It is evident there is considerable variation in the rate of growth in nature, from the difficulty of distinguishing in a large number of fish those of one year's, two years', and three years' growth" (Cunningham 1891:97).

C. G. J. Petersen, director of the Danish Biological Station, may be best remembered today for his pioneering efforts with fish marking and the mark-recapture population estimate method that bears his name (it has been argued that Petersen never used his marking methods to conduct a population estimate, with priority instead going to Knut Dahl, a member of Johan Hjort's staff in Norway; Le Cren 1965). Petersen's work using lengths to assign ages to blenny (*Zoarces viviparus*) received more notice than Cunningham's, but was characterized by the same difficulties (Petersen 1892, summarized by Ricker 1975). Petersen constructed what are now known as length-frequency graphs, proposing that the peaks, or modes, that were evident across the range of smaller to larger size classes represented progressively older age-classes of fish. Petersen's approach suffered the same sensitivity to variability in growth rates as had Cunningham's less quantitative presentation. Modes became difficult to differentiate for older age-classes and overlap in lengths of fish between the modes made confident assignment of ages to fish based on length alone problematic (see Allen 1917; Smith 1994).

Following the papers of Hoffbauer and Reibisch, fish aging began to be featured in many of the fisheries assessments in the early 1900s. Michael Graham, the research director at Lowestoft responsible for recruiting and mentoring, among others, Raymond Beverton and Sidney Holt, recalled that the "majority of workers showed no scepticism [sic]" (Graham 1943:134). Graham included among those who were skeptical C. J. G. Petersen, who during lunch "once asked an ardent believer in the new method if it included the rings on the slice of beetroot on his plate" (Graham 1943:133-134). The validity of aging techniques was questioned by some workers, in some cases pointedly (e.g., Williamson 1918), and refinements of methods continued. These debates did not, according to existing contemporary accounts, slow the incorporation of aging into studies of most of the major fisheries (see Allen 1917; Van Oosten 1929).

A notable early debate concerning the application of age data centered on the work of Johan Hjort, a respected figure in Norwegian fisheries studies who assumed a lead role in the International Council for the Exploration of the Sea when it was established in 1902 (Rozwadowski 2002). Hjort recounts having seen Heincke present results of his work on fish aging to the council in 1904, after which Hjort arranged to visit Heincke at his laboratory to learn more (Hjort 1914). Hjort soon put his assistants to work developing an extensive aging program, settling on scales as his primary tool. His goal was to frame his fisheries research in light of the science he referred to as "vital statistics," or what we would now call demographics, with the explicit intention of collecting "representative statistics" that would allow insights into "1. Birth-rate. 2. Age-distribution. 3. Migration" (Hjort 1914:11).

Hjort presented his plans for the use of scale-based age determinations in assessing herring populations to the council in 1910, initiating a debate about the validity of the scale method that was spearheaded by D'Arcy Wentworth Thompson, the British delegate to the council (Smith 1994; Rozwadowski 2002). Thompson's concerns carried the day, and Hjort's proposed program of study was not supported by the council. Hjort continued his work anyway. Hjort's assistant, Einar Lea, who was by this time leading the lab's scale studies, continued to present results of their work and invited other scientists to demonstrations of the method, and ultimately the council appointed Hjort as chair of a committee charged with further assessments of the new method, a committee on which Thompson was not included (Smith 1994; Rozwadowski 2002).

The results of Hjort's research program were laid out in his 1914 monograph *"Fluctuations in the great fisheries of northern Europe viewed in light of biological research"* (Hjort 1914; Figures 4–5). Today this paper is most often cited in reference to Hjort's hypothesis that the concept of a critical period in the early life history of fish developed by Fabre-Domergue and Biétrix (1897) in aquaculture settings could apply to wild fish populations. However, Sinclair and Solemdal (1988) point out that the contemporary impact of Hjort's research related to his use of age data to link variability in landings to variable recruitment within fish populations. While commonly accepted today, Hjort's insights were revolutionary in their time, and would lead to fundamental changes in how fish populations were studied and fisheries managed.

Hjort's paper received a glowing notice in the journal *Nature* from E. J. Allen: "There can be little doubt that this report by Dr. Hjort will mark an epoch in the history of scientific fishery investigation" (1914:672). The praise was not unanimous. D'Arcy Wentworth Thompson, best known as a biomathematician and author of the classic *On Growth and Form*, responded to Allen's review expressing his inability to accept Hjort's conclusions (Thompson 1914a, b). Thompson did not accept Hjort's conclusions that the 1904 year class dominated the Norwegian spring herring fishery for more than 5 years. His doubts were based in part on his feeling that the "assumption" that the ages of herring were indicated by rings on the scales was far from proven and also on his belief

Figure 4. Photograph of a herring scale from Hjort (1914).

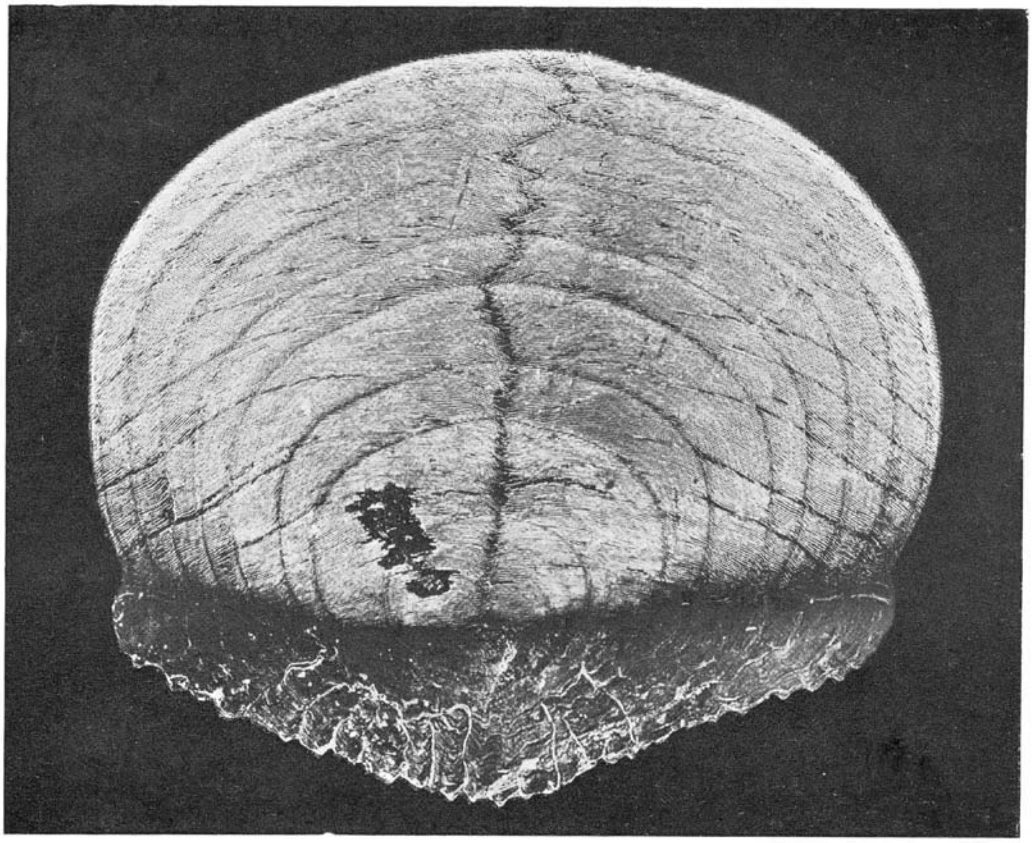


Fig. 9. Herring scale with 8 winter rings inside the edge (Lea phot.).

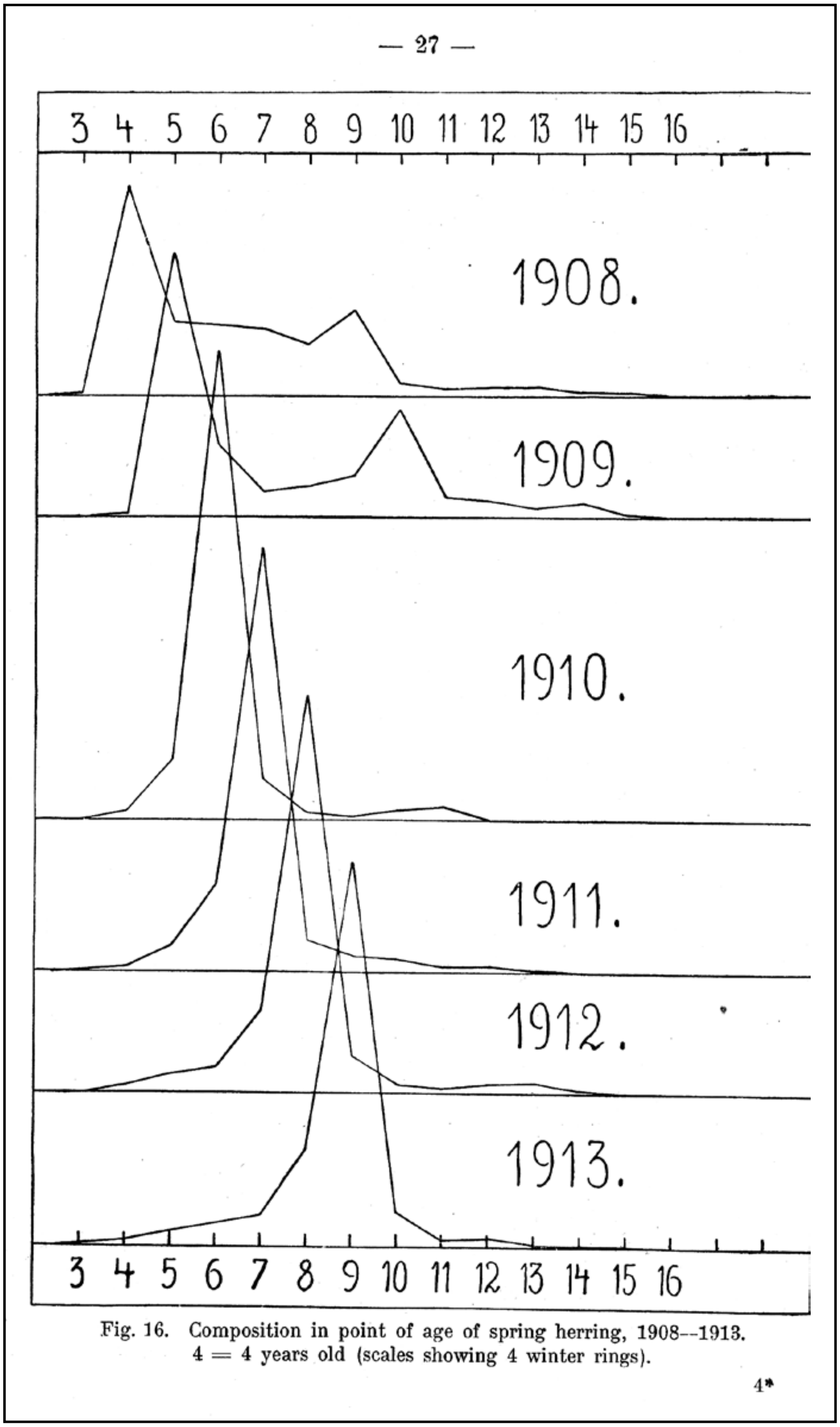
that same-aged fishes tended to shoal together. Thompson noted that the frequency distribution of herring age groups in Hjort's data "ranged themselves with great apparent regularity in a unimodal skew-curve." (Thompson 1914a:60). He argued that the conclusions drawn from Hjort's age distributions were "statistically improbable," and used that improbability to conclude that the rings on herring scales were unlikely to vary in number as a function of age: "Just as the individual herrings vary in a normal fashion about a certain modal size, so do they also vary, in the number of their scale-rings, about a certain modal number." (Thompson 1914a:60). Thompson finished by describing Hjort's efforts to interpret his data as "a clear case of a biological problem, based upon statistics, surrounded by mathematical difficulties, where the biologist cannot possibly be sure of his ground until he has enlisted the help of the mathematical statistician" (Thompson 1914a:61).

Hjort enlisted his assistant Einar Lea, who had conducted the bulk of the aging studies on herring and had previously published his methods in detail, in his response to Thompson's criticisms (Hjort and Lea 1914). They began by reiterating their methods for age determination using scales and emphasizing the amount of evidence from other sources that the method was valid. They then addressed Thompson's statistical concerns by presenting comparisons of a normal curve to their age-frequency curve, concluding that "the dissimilarity of the two curves is, in fact, so great as to exclude any idea of the age-curve following the usual law of biological variation" and that "it seems to us impossible to explain the observed facts as a result of common variation, even if the help of a mathematical statistician were enlisted." (Hjort and Lea 1914:256). Thompson's follow-up letter, raised additional concerns about sampling issues and sample sizes in Hjort's studies, and reiterated his "unaltered incredulity" (Thompson 1914b:363). History would bear out the soundness of Hjort's science, although Thompson would remain firm in his skepticism about the reliability of scales for aging herring until 1930, when he publicly announced his conversion at an ICES meeting (Smith 1994). Thompson's arguments did bring attention to the need to obtain samples from multiple locations and schools of fish if the intention was to characterize the age composition of the entire stock (Smith 1994). Perhaps ironically, just three years after his debates with Hjort, Thompson's analyses of the length composition from his commercial port sampling of haddock catches would add to the growing body of evidence that fish populations exhibited large natural fluctuations in recruitment (Smith 1994).

The incorporation of age data in studies of freshwater fish populations progressed more slowly than it did in the studies of marine populations. Carlander (1987) theorized that the delay was partly attributable to limited communication among freshwater and marine fisheries scientists, but was in large part due to the focus on stocking and habitat in freshwater management rather than on issues of harvest and yield where age data were particularly valuable. A. G. Huntsman of the Fisheries Research Board of Canada was keeping abreast of the developments in Europe, however, and in 1918 presented a paper to the Royal Society of Canada on its potential applications, soon followed by a similar presentation to the American Fisheries Society (Huntsman 1918, 1919). Carlander (1987) credits Huntsman's papers with bringing aging methods to the attention of North American workers, and the first papers in the *Transactions of the American Fisheries Society* applying the methods to freshwater studies appeared in 1924. Borodin (1924) used scales to assess American shad (*Alosa sapidissima*) in the Connecticut River, and a study of the use of otoliths in the same system followed soon after (Barney 1924). A search of articles in the *Transactions* reveals only one other application of aging to fish studies in the 1920s, but an increase to 84 in the 1930s, 74 during the 1940s, 112 during the 1950s, followed by rapid increases to 231 in the 1960s and 370 during the decade of the 1970s.

The foundations for routine incorporation of age data into fish population assessments were well-established by the early years of the 1900s. The structures used to perform the majority of current agency aging of freshwater fishes in North America had all been introduced into the literature prior to 1925. New techniques frequently encounter resistance upon their initial application, and fish aging was no exception. While contemporary accounts suggest that aging techniques were adopted quickly and widely after their discovery by the fisheries profession, controversies, both private and public, did occur. Hopefully, the preceding review of the earliest works on fish aging and their early impact on fisheries research will help readers appreciate the foundations upon which current aging programs have been built, and serve as a useful documentation of the primary literature for those techniques covered in the review of current practices presented by Maceina et al. (this issue).

Figure 5. Age frequency graphs of herring based on scale ages from Hjort (1914).



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