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NOAA-TM-NMFS-SWFSC-223

U.S. DEPARTMENT OF COMMERCE
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U.S. DEPARTMENT OF COMMERCE
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TABLE OF CONTENTS

Table 1- History of Pacific sardine age determination

Author/Date	Accomplishment
Godsil (1932)	Aged sardines successfully using both scales and otoliths, unpublished manuscript.
Clark (1936)	Rejected the use of hard parts to age sardines; instead identified modes in length frequency distributions to separate year classes.
Walford and Mosher (1943)	Proved validity of scales and otoliths for ageing younger fish, but recommended scales as the preferred method for older fish.
Felin and Phillips (1948)	Joint program undertaken by the U.S. Fish and Wildlife Service and California Division of Fish and Game to gain a comprehensive sardine age composition for CA, OR, WA and British Columbia using scales during 1941-1947 (based on recommendation from 1943).
Mosher and Eckles (1954)	Extracted a set of both scales and otoliths from fish taken in December 1942 from San Franscico to prove comparable results of both methods; with this knowledge, expanded historic age composition of fish from 1930-1938, a period from which only otoliths were collected.
Gates and Wolf (1962), Wolf and Daugherty (1961), Phillips (1948), Kimura (1973), and others	Determined age composition of catch from central and southern California and Baja using scales between 1948 and 1965.
Butler (1987)	Demonstrated the formation of daily growth increments in sagittal otoliths.
Barnes and Foreman (1994)	Use of otoliths from random stratified port sampling program to attain age composition from the San Pedro wetfish fishery. Validated the formation of one opaque and one translucent growth increment per year.

I. Introduction

The California sardine fishery is replete with historic quantitative data including catch statistics, biomass estimates, length-weight relationships and age composition of landings. The methodologies employed to calculate these estimates were well-documented. However, methods for age determination of individual sardines were often overlooked, or if discussed lacked detail and were rarely illustrated. The method currently employed by the California Department of Fish and Game (CDFG) to estimate sardine age by counting annual increments on sagittal otoliths is documented in this paper. Results of these ageing techniques are substantially consistent with those used in previous sardine age composition studies where ageing methodology was not clearly defined.

It has long been accepted that ring formations visible on scales, otoliths, fin spines and rays, opercles, vertebrae and other bones serve as a record of the life history of each individual. Examination of these structures can be used to approximate age at the time of capture for many fish species. However, only by labor-intensive daily growth increment studies or monitoring hatchery-reared fish of known age with mark-recapture techniques is there an accurate method to determine the exact age of fish landed in a commercial fishery. Age composition of the sardine population is utilized in age-structured population models to generate biomass estimates and set the allowable harvest.

Randomly stratified port sampling of the commercial catch of sardines is currently conducted by CDFG. Thousands of individual sardines are collected and their length, weight, age, and sexual maturity determined. Enumeration of annuli in otoliths offers an accurate and rapid method of determining age. Although counting annuli involves reader subjectivity, it serves as a valuable tool for estimating age when other more precise means are not feasible or practical, and provides sufficient accuracy to develop a database for age-structured population models such as CANSAR. An experienced annulus reader is capable of ageing approximately 30 fish per hour using the described methodology, while counting daily increments can take many hours to reach an age determination for a single fish.

II. History of using otoliths to determine the age composition of sardine

Unlike some commercial fisheries, age composition of sardine landings in California is relatively well documented for most of the 20th century (Table 1). One of the earliest attempts to derive age estimates from the sardine fishery was by H.C. Godsil (Felin and Phillips, 1948). Between 1928 and 1933, he obtained specimens from the southern California fishery and compared age estimates determined from annuli on otoliths to those obtained from scale analysis. He compared those results with length-frequency analysis and concluded that otoliths provided the most reliable age estimates (Godsil, 1932 ms.). He found that alternating translucent and opaque zones within the otolith are deposited seasonally; that opaque deposition occurs in May, June and July; that a "dark zone" is formed from about November to March; and that fish of the year and young sardine in general may exhibit a "transitional" type margin into late autumn. However, no attempt at this time was made to use margin classification for validation that annuli are deposited once each year (Barnes and Foreman, 1994).

Despite these data, Clark (1936) contended that age composition of sardine was only attainable through analysis of length-frequency data, the most common method to attain an age composition at the time, and denounced both scale and otolith reading techniques as unsuccessful in sardine. Although length-frequency is usually adequate to determine the age of fish at young ages, increasing overlap occurs in older age classes (Everhart and Youngs, 1981).

Consequently, age determination using otoliths and scales was considered "unsatisfactory" by those later attempting to attain age composition data (Felin and Phillips, 1948) and use of the technique was abandoned until the mid-1950's (Mosher and Eckles, 1954).

However, ageing sardines using scales and otoliths was not permanently quelled despite Clark's early criticism. Evidence that sardine otoliths could be used as an accurate indicator of age was reaffirmed when Walford and Mosher (1943) demonstrated that age determinations from scales were highly correlated with estimates from otoliths and length-frequencies in fish taken from the southern California fishery in 1938-39. Of 1036 fish aged by both scale and otolith methods, they found 98 percent agreement on age in years for fish with one annulus present, 92 percent for fish with two annuli, and 75 percent for fish with three. However, they considered the use of scales as more reliable and the preferred method for determining an age composition of the fishery, as they appeared more readable in older aged fish, and preparation techniques were simpler (Felin and Phillips, 1948). Walford and Mosher concluded that the first two year-marks on otoliths were generally well-defined, the third less so, and subsequent ones were so closely crowded that they were easily confused with false year marks.

The U.S. Fish and Wildlife Service and the California Division of Fish and Game began a joint comprehensive study of sardine age composition during the 1941-42 fishing season. The agencies selected scale analysis as the method for age determination (Felin and Phillips, 1948) based on recommendations from Walford and Mosher. This program continued through the 1965 season, when collapse of the sardine fishery ended their need for extensive age composition analysis.

The question of otolith validity for ageing was resurrected by Mosher and Eckles (1954). They analyzed data from 473 fish collected from the San Francisco commercial fishery during the 1942 season. Comparison of ages determined from both scales and otoliths from the same fish demonstrated that otoliths were as reliable as scales for determining age. Age composition of commercially-caught fish from San Pedro and Monterey between 1930 and 1938 was subsequently determined from otoliths. Because no scales were collected during this period, analysis of otoliths served to significantly extend the historical database of the sardine age composition, and reinstated their use in the monitoring program.

Between 1974 and 1985, a moratorium was placed on the California sardine commercial fishery, and therefore no age composition data were collected during that time. Once the moratorium was lifted, a randomly stratified sampling program was established by CDFG for the commercial wetfish fishery to collect otoliths for age determination (Wolf, 1987). Age composition and other fishery data attained from this program have been used to monitor population trends and abundance during the current period of stock recovery (Barnes et al, 1992).

Otoliths have also been used to validate daily growth in juvenile sardines (Butler, 1987). Barnes and Foreman (1994) used these data to validate that annuli visible on the otolith are, in fact, deposited annually in conjunction with seasonal change. The presence (or absence) of an annulus was found to correspond with hatch date back-calculated from counting daily growth increments for fish up to 1.5 years of age. For older fish, opaque margins characteristic of periods of rapid growth were shown to be prevalent in the summer and early fall months, while translucent or slow-growth margins were displayed most often during the winter months.

Otolith analysis is currently the preferred method for determining age of sardines for several reasons. 1) The age composition is derived from samples randomly collected as fish are unloaded for cannery processing, and in general, all scales have been inadvertently removed by handling; 2) Unlike scales, sardine otoliths do not require mounting or other preparation prior to examination, and are stored with relative ease; 3) CDFG wetfish sampling programs using otolith examination were already in place for other species, specifically, similar techniques were used for ageing northern anchovy (Engraulis mordax) (Collins and Spratt, 1969) and Pacific mackerel (Scomber japonicus) (Fitch, 1951). Consequently, when CDFG's wetfish sampling programs were unified and revised, otoliths were selected for analysis of all species.

III. Extraction, Setup and Equipment

In most fish species, the sagittal otolith in the sacculus is the largest of three pairs of otoliths located in the labrynth system (Blacker, 1974), and is the one used for age determination of sardines. Otolith extraction is relatively simple, requiring one cut in the skull behind the eyes, exposing the brain and membranes surrounding the sagittal otoliths (Jearld, 1983).

Following removal, otoliths are cleaned of any blood or tissue, and rinsed in distilled water. Using fine forceps to prevent crushing the otolith and to improve precision in handling, otoliths are air dried on a paper towel. Each pair is stored in a labeled gel capsule. Readability of sardine otoliths when stored dry is acceptable, unlike otoliths of other species that require storage in glycerin or other liquid medium. Although little information exists on long-term effects of dry storage of sardine otoliths, archival samples of dry anchovy otoliths located at the Southwest Fisheries Science Center showed no change in readability over 14 years.

Otolith pairs are submerged under 4-5 millimeters of distilled water in a watch glass with black background to improve clarity. Using a stereoscopic microscope at 12-25X magnification and reflected light, opaque increments appear white, and translucent increments appear black or gray. If transmitted light is used, opaque depositions on the otolith disrupt light passage, and appear as dark regions, while translucent increments allow the penetration of light and appear white. Magnification should not be changed during examination as it is important to maintain consistency to maximize precision.

Increment distinction is usually most pronounced in the posterior region of the external (proximal) otolith surface (Figure 1). Age should not be determined from otoliths that are deformed or have incomplete opaque deposition (Blacker, 1974). It is not uncommon for one or both members of the pair to be somewhat deformed; therefore both otoliths should be examined (Figure 2). Readability of the pair is usually improved if placed in the watch glass side by side, sulcus side down (Figure 2), as annual increments may be more distinct on one otolith than the other.

Otoliths should be read within three minutes of initial immersion because water is quickly absorbed. Once saturated, the outermost opaque increments tend to fade or become indistinct from translucent zones, reducing the reliability of age determinations with increased soaking time.

IV. Otoliths as records of life history

Otoliths serve as permanent temporal records of the lifespan of individual fish. Unlike other body parts, otoliths are not resorbed in times of stress, and continue to grow throughout their life. Each year, sardines deposit one opaque and one translucent increment. Opaque zones reflect periods of rapid growth, corresponding with summer months when food is abundant and growth conditions are most favorable. Translucent increments correlate with periods of reduced growth (Beckman and Wilson, 1995).

Otoliths consist of a lamellar crystalline matrix of protein and calcium carbonate in the form of aragonite (Pannella, 1974).

During periods of active growth, higher water temperature and abundant food, more proteinaceous organic material is deposited in the otolith, defining the opaque increment. The calcium carbonate crystals in translucent increments are larger, with only a small amount of intercrystalline protein, producing a relatively clear appearance (Irie, 1960, Beckman and Wilson, 1995).

The locality of deposition of calcium carbonate in otoliths also differs, as most new material is placed on the outermost edges and ventral surfaces surrounding the sulcus. Deposition occurs almost exclusively in these regions in older adult fish (Irie, 1960).

This pattern of seasonal opaque and translucent deposition has been validated for sardines (Barnes and Foreman 1994), jack mackerel (Trachurus symmetricus) (Knaggs and Sunada 1973) and many other fish worldwide (Beckman and Wilson 1995). There is evidence in other species that opaque deposition is instead correlated with times of stress such as spawning or reduced growth (Blacker, 1974). Historic literature studies by Blacker (1974) Pannella (1974), and Beckman and Wilson (1995) comparing opaque deposition to translucent deposition indicate that the phenomenon varies by species and location.

Depositional patterns may also differ between populations of the same species. Pacific sardine populations in more tropical environments may or may not show annual depositions on otoliths, as exhibited by those located in Magdalena Bay, Baja California

Sur, Mexico. Unlike their northern counterparts, fish from this population form increments semi-annually, likely a response to spawning stress (Felix and Ramirez, 1989).

Because of a reduction in the effect of seasonal changes in growth, fish in more tropical environments frequently deposit translucent zones in response to lunar activity and reproductive stress (Pannella, 1974), as opposed to the annual depositions associated with seasonal changes for more temperate fishes. In the South West African pilchard Sardinops ocellata, translucent deposition considered to be the "annulus" forms between September and December, and is likely associated with the spawning peak. However, as many as three other distinctly translucent "secondary rings" (or check marks) form at various times during the year (Thomas, 1984).

Because sardines are a relatively short-lived species, examination of the external surface of the otolith is a satisfactory technique for determining annual growth increments. Because sardines have a relatively low survivorship (M= 0.4, McCall, 1979), the otoliths do not require cross-sectioning or other preparation necessary for species with thick otoliths containing numerous annuli. Otoliths from cod, for example, do not form annual increments equally on all surfaces. As it grows, the cod otolith increases more in thickness than in length, so that observation of the exterior surface of the otolith will not reveal the true age. Consequently, cross-sectional analysis of cod otoliths is necessary (Chilton and Beamish, 1982).

Although the timing of annulus formation can vary, most sardines exhibit opaque deposition during July through October and translucent deposition during the remainder of the year (Barnes and Foreman, 1994). Age 0 and age 1 fish, however, tend to exhibit opaque deposition earlier in the year and may exhibit zones not clearly translucent or opaque, correlated with growth occurring in winter.

During the first few years of life, opaque increments tend to be significantly wider than adjacent translucent increments, which represents a rapid otolith growth rate. With age, opaque depositions become increasingly narrow, and at some point become nearly the same width as translucent increments, which remain fairly uniform in width over age (Williams and Bedford, 1974).

As sardine otoliths grow, some deposition occurs across the entire otolith surface, but a state of either opaque or translucent deposition is clearly identified at the posterior margin. As the fish continues to age years, the otolith thickness increases as the sulcus side deposition becomes more extensive. Additionally, grooves and spiny protuberances on the ventral side of the otolith become more pronounced.

V. Methodology of otolith examination

An annulus is defined by Secor et al (1995) as one of a series of concentric zones on a structure that may be interpreted in terms of age. It is either a continuous translucent or opaque zone that can be seen along the entire structure or as a ridge or groove in or on the structure. Although useful, Secor et al's (1995) definition is quite general. Age determination by CDFG requires a more precise definition of an annulus that distinguishes the point at which age should be enumerated to reduce ambiguities in ageing criteria, as the first year of growth is represented by one complete opaque and one complete translucent increment. Specifically for this work, the annulus is designated as the interface between an inner translucent growth increment and the successive outer opaque growth increment (Fitch, 1951).

By counting successive annuli, an age and year class of fish can be assigned (Figure 3). By convention, a year class consists of all fish hatched during a calendar year. Although some sardine spawning takes place year-round, the majority occurs in early summer (Figure 4). Because actual hatching date for each individual is unknown, it is assumed that all individuals hatched during a calendar year are born on July 1.

When estimating age from otoliths, the capture date is essential to assign the proper year class. A fish caught in the first semester has not reached the common July 1 birthdate, therefore the most distal pair of opaque and translucent depositions are not counted. For example, a fish captured on June 9, 1995, that displays a full opaque increment in the center followed by a translucent increment (even if exhibiting the early beginnings of a second opaque increment) is assigned an age of

zero, and designated a member of the '94 year class. If that same fish was caught on July 9, 1995, it would be assigned an age of **one**, and would still be considered as part of the '94 year class.

In addition to assigning an age and year class, the margin is classified as opaque or translucent, wide or narrow (Jensen, 1965) and a confidence rating is assigned to the age estimate. If the reader is very confident the assigned age is the true age of the fish, a confidence rating of zero is issued. If the reader is fairly certain the age assignment is correct, but feels that another experienced reader could interpret the increment structure differently and reach a different age conclusion, a confidence rating of one is assigned. If the reader can only make a rough estimate of age due to irregular or indiscernible features, a confidence rating of two is assigned.

Although CDFG does not use confidence ratings to weigh the accuracy of age estimates, the information is useful when comparing precision between readers. Even if a low confidence rating is warranted, it is crucial that an age is assigned to all fish. Older fish are often more difficult to age and are a smaller fraction of the population, and if readers fail to make estimates for these fish a biased age composition may result.

Examination of historic literature shows that current CDFG ageing interpretations are consistent with our prior methods, with the following exception. Walford and Mosher (1943) defined the "year mark" (or annulus) as the inner edge of the translucent zone. The current understanding is that the translucent zone is deposited throughout the winter, or slow-growth period, and thus should be completed before adding another year to the age.

VI. Interpreting otolith structure

Although the concept of counting annuli is straightforward, the interpretation of the otolith's appearance may cause difficulty. Because every otolith has different markings, determining whether or not a structure is indeed an annulus may be difficult. It is simply a matter of interpretation, and is often considered more of an art than a science (Williams and Bedford, 1974). It is commonplace for experienced readers to admit that one or more different age conclusions may be reached from a specific otolith.

Many otoliths exhibit check marks, or discontinuities in a zone or in a pattern of opaque and translucent zones (Secor, 1995). These are often deposited in response to individual physical stress due to environmental conditions other than seasonality (Figure 5). Although these marks are clearly visible, they do not indicate seasonal growth. If not recognized as a check, they will cause an overestimation of age.

Commonly reflected patterns in many otoliths can help a reader reach an age estimate. The following principles may be helpful in interpreting the structural appearance and discerning annuli from checks:

A. A seasonal pattern is displayed in the margins of most sardine otoliths. Opaque deposition usually occurs from June through October, while translucent growth tends to occur during the rest of the year (Figure 6 and 7). In fish aged zero or one, however, opaque deposition may begin earlier and end later reflecting more extensive growth in earlier years of life. Because capture date is known, classification of margin condition as opaque or translucent, wide or narrow (Jensen, 1965) can assist the reader in assigning a year class.

B. Spacing can often be used to distinguish true annuli from check marks. As juvenile fish increase in age, reduction in growth rate of the otolith is commonly exhibited by a narrowing of the opaque increments toward the margin (Figure 2). However, in fish older than age two, annuli present beyond the first or second year may be spaced fairly equally (Figure 5).

C. Position of marks relative to the focus is critical for determining their significance. In the first year of growth, for example, a wide opaque deposition near the focus broken by a fine translucent increment is likely to be considered a check during the first summer's growth. If the same mark were present in a more distal location on an older fish, it would be more likely interpreted as an annulus. Toward the margin, any visible mark has increased significance. In fish of age five or older, for example, the outermost opaque increments may barely be visible, and in fact, may be so faint that only a slight haze is apparent to discern them from translucent increments.

D. Reading is occasionally improved by rotating the otolith to stand on its ventral side to obtain a surface-relief view of depositions. Opaque growth tends to be heightened above the translucent zones, creating the appearance of peaks and valleys in the surface of the otolith (Figures 2 and 8).

E. Otolith size cannot be used to estimate age of fish, although it can be useful to distinguish an age five fish versus one that is zero. Like otolith size, the otolith length or radial distance from the focus to the margin cannot provide an accurate age, as depositional growth on the otolith and somatic growth of the fish do not occur at the same rate.

F. There may be checks within annuli or patterns of deposition distinct to specific year classes or fish from a specific location. Conversely, otoliths from fish of the same year class may have vastly differing appearances (Figure 9) in terms of patterns, condition of the margin, or presence of check marks, but they still exhibit the same number of annuli.

G. During the first year of growth, opaque deposition may continue into the winter months, and instead of a clearly defined translucent zone, opaque deposition seems to become less distinct, appearing grayish in color under reflected light (Figure 10). It is easy to confuse this reduced opaque deposition with a true annulus, especially when spacing is concurrent with successive annuli.

Although characteristics noted above are useful in reaching age estimates for many fish, they are not conclusive in all cases and exceptions are commonplace. For example, occurrence of an opaque margin in February is atypical, although it does occasionally happen (Figure 9C). Likewise, an otolith may exhibit a wider opaque zone during the second summer of growth than the first, possibly initiated by a late spawning date. It is important for the reader to be consistent in applying criteria with regard to patterns. There is no way to learn the art of interpretation other than by repetition and experience, and it usually requires examination of over 1,000 otolith pairs before acceptable proficiency is gained and nuances recognized (Figure 11).

VII. Areas for further research

Additional work is being done by biologists from National Marine Fisheries Service, CDFG and Instituto Nacional de la Pesca biologists to refine and improve the precision of age determinations.

One promising technique is analysis of otolith weight (Fletcher, 1991). Hopefully, a direct relationship between otolith weight and age can be found, thereby providing an objective rather than subjective method to assign age.

Because fish growth is most rapid during the first year of life, otolith deposition is also most extensive at that time. Research is currently underway to determine an average or a minimum distance to the first annulus by measuring the length from the focus to the end of the first translucent zone. From these data, new criteria may be established to standardize methods of interpreting otoliths displaying check marks within the first year of growth.

However, any improvements or changes to our ageing criteria must first be validated. Fortunately, daily growth increment data provide a direct way to evaluate new hypotheses for interpreting sardine otoliths, as a more precise age of the fish in days can be accurately determined. With this information, true annuli can be confirmed and distinguished from check marks, and relationships between otolith weight and age assessed.

View of a Typical Sardine Saggital Otolith

External (proximal) side up; sulcus side down

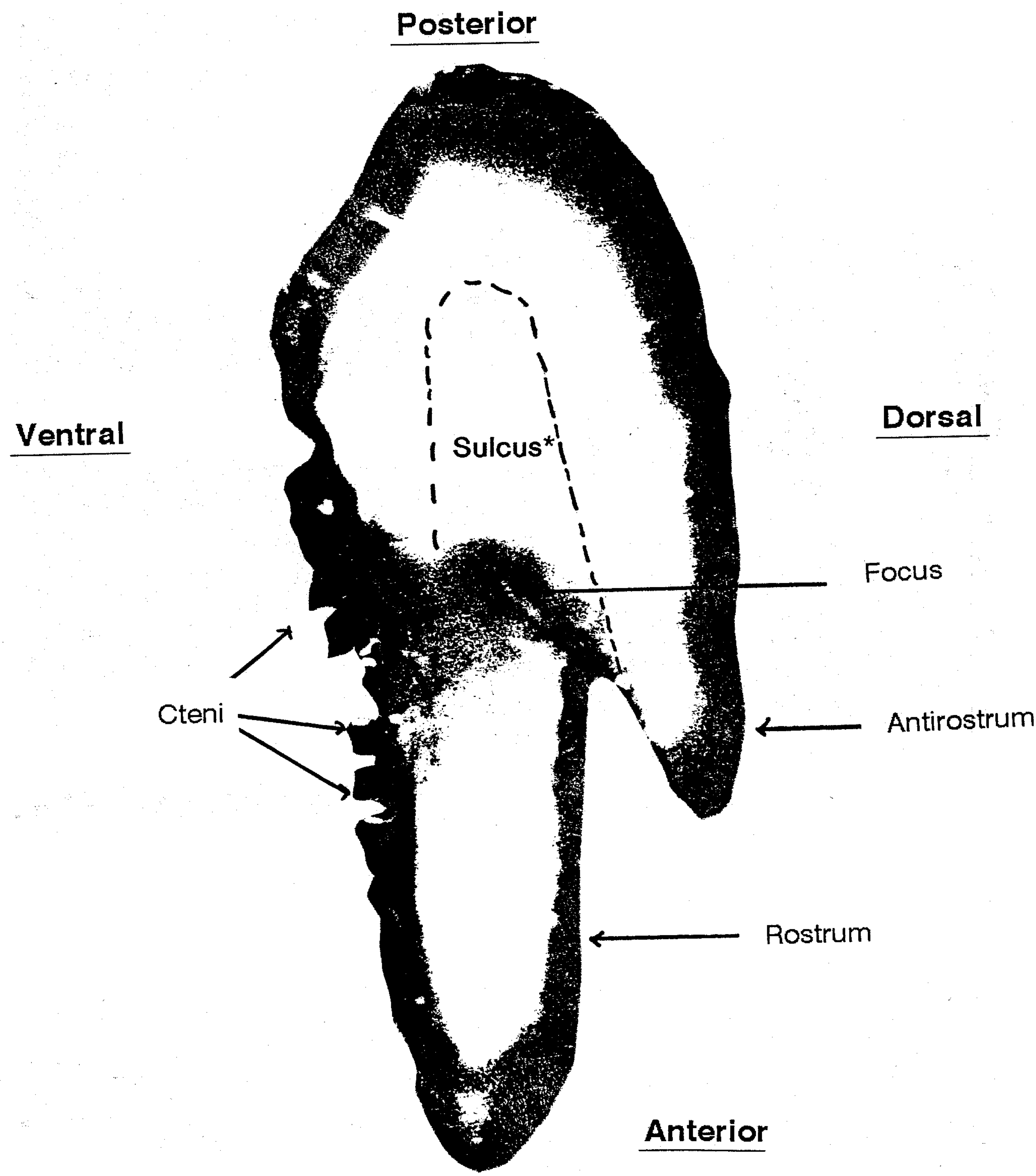


Figure 1

* The sulcus is visible only on the distal (internal) surface of the otolith.

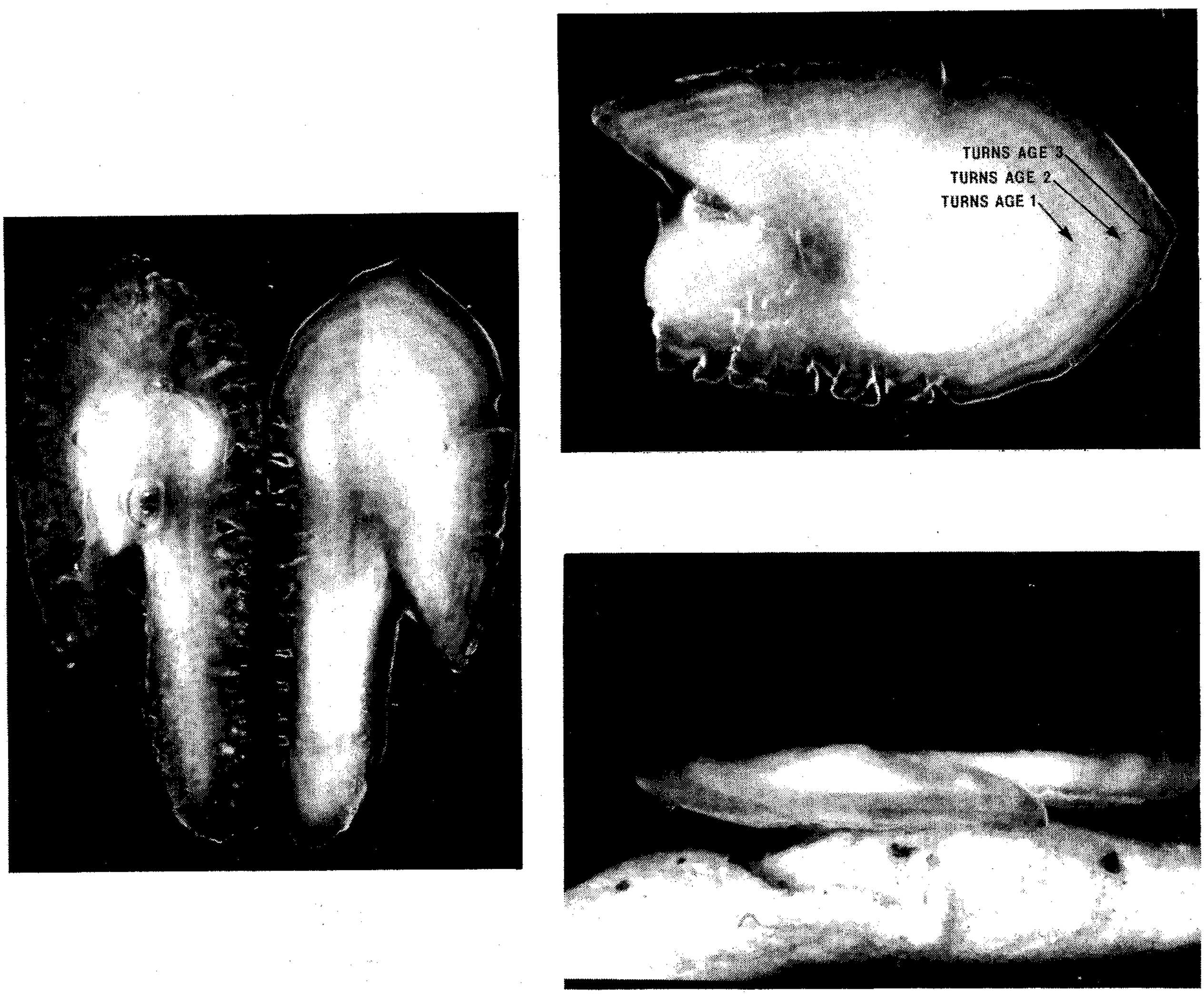


Figure 2.

(A) The left otolith of this pair is deformed, and should not be used to reach an age determination. Both otoliths here display the sulcus side up.

(B) The readable member of this otolith pair is reoriented so the sulcus side is down. The rostrum has broken off due to handling. Note the improvement in the distinction of the increments. Captured in the first quarter of 1995, this fish is of age three. Observe the width of the opaque increments decreases distally, while the translucent increments remain fairly consistent.

(C) A three-dimensional view of the otolith displays the opaque increments as elevated above the translucent increments.

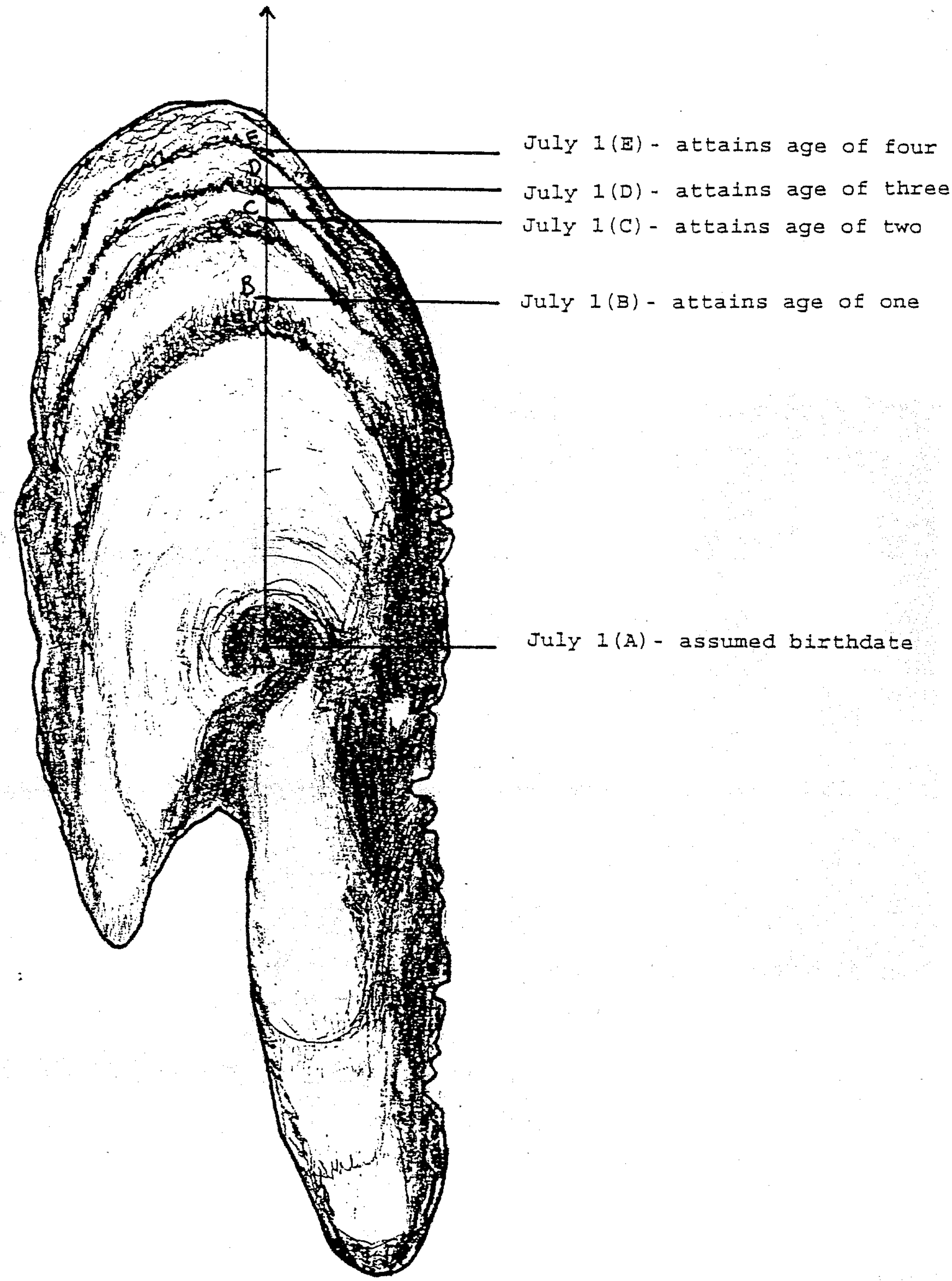


Figure 3. Diagrammatic representation of a Pacific sardine otolith showing four distinct annuli, recording a permanent record of the individual's growth over its lifetime from the focus to the margin. As depicted, the margin is classified as opaque-wide, typical of a fish captured during late summer or early autumn. Were this fish to extend its lifespan, on the next July 1 it would have a fifth birthday. At that time, the otolith would exhibit another full translucent increment and the beginnings of another opaque increment would likely be apparent at the margin.

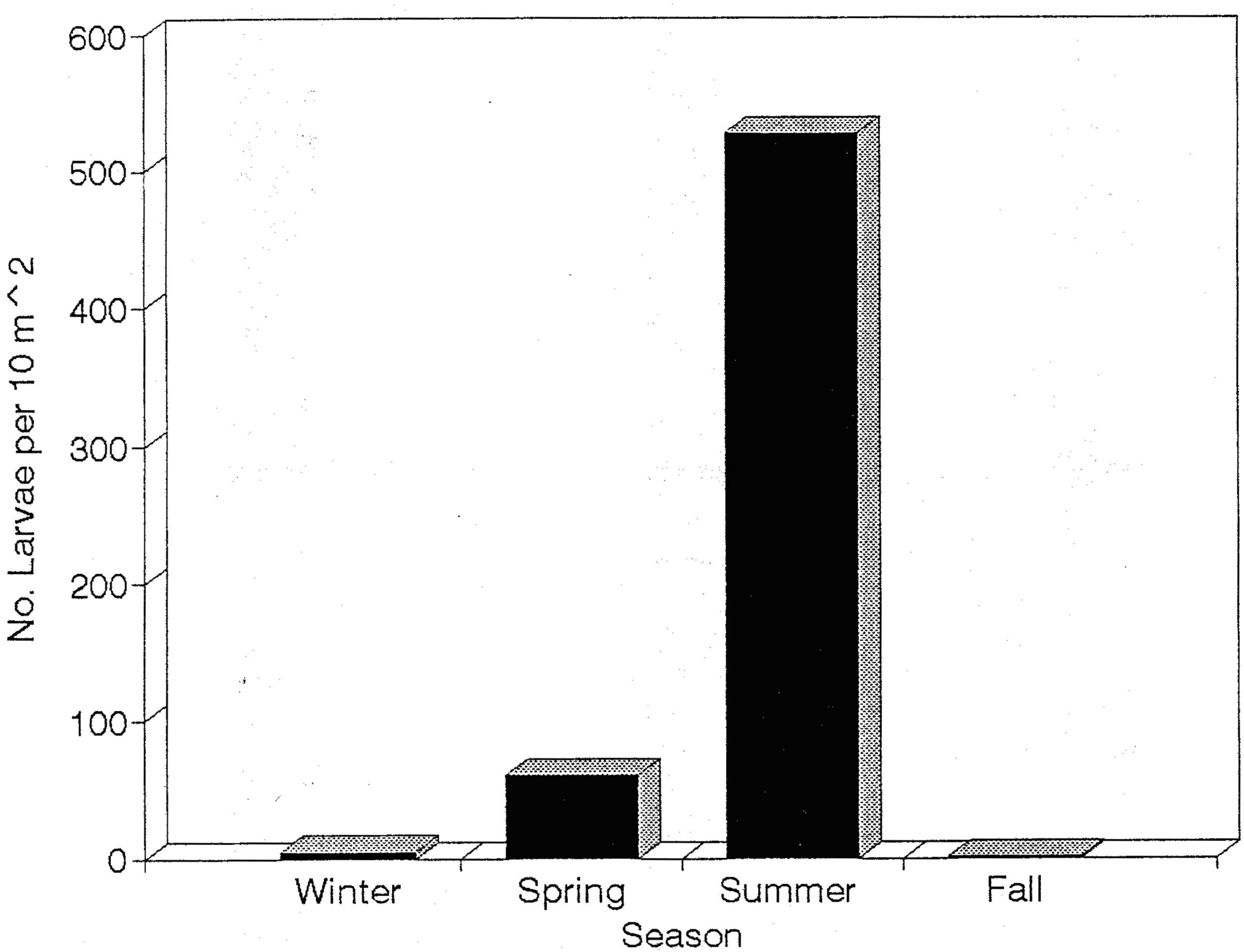


Figure 4. Seasonal distribution of sardine larval density. Data were summaraized from CalCOFI cruises during 1984-1993. A summer spawning peak is clearly evident, forming the basis for the assumption of a July 1 birthdate. Winter is defined as January-March, spring as April-June, summer as July-September, and fall as October-December.

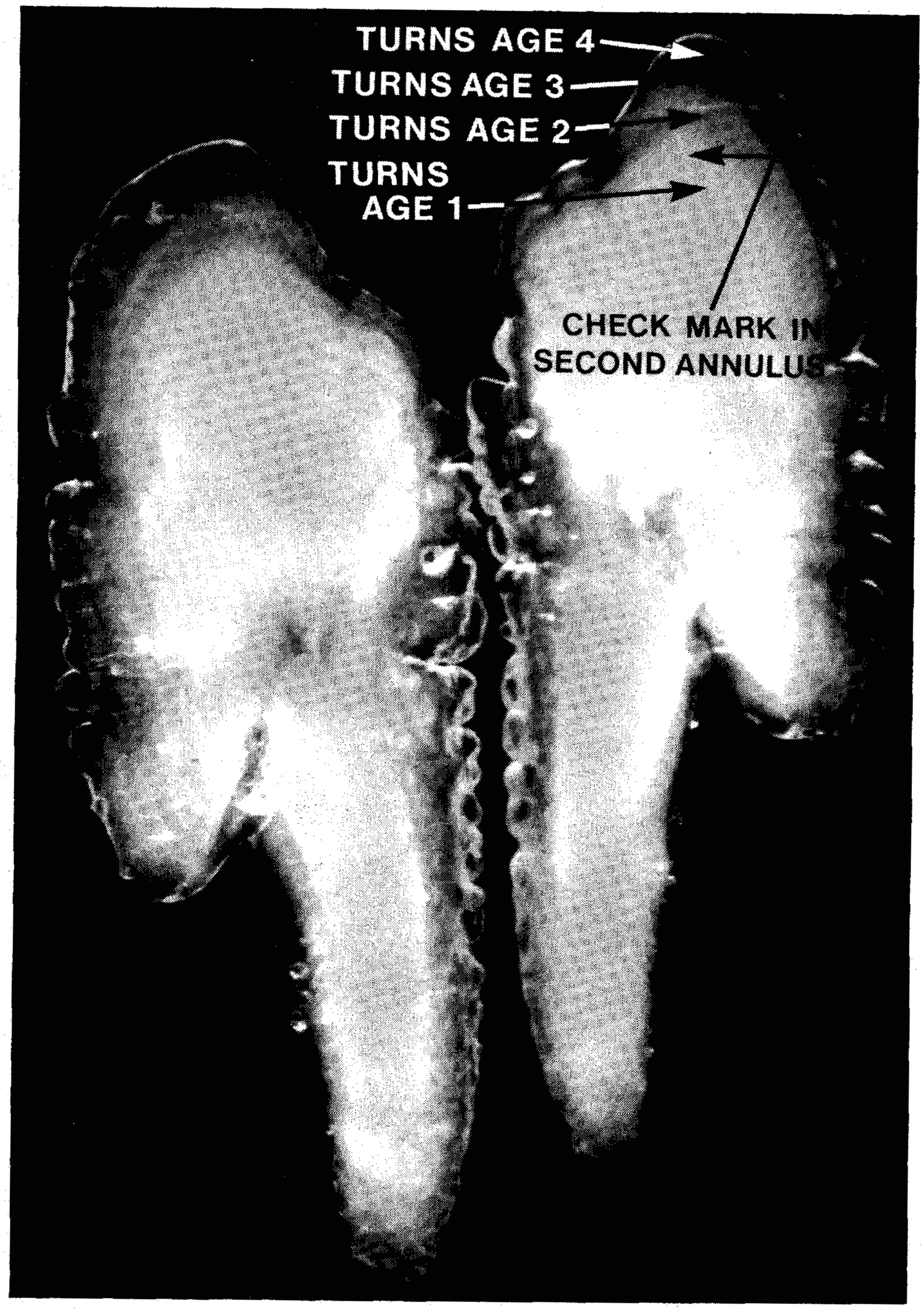


Figure 5. Sardine otolith with four annuli, captured in the first quarter of 1995. A pronounced check mark is visible in the second annulus. Distinction is reduced between the first opaque and first translucent increments as successive layers are deposited, causing increased thickness of the otolith toward the focus. Note the decrease in width of the opaque increments as deposition occurs distally, reflecting slower growth rates in later years of life. The margin is classified as translucent-wide, as is expected considering the capture date.

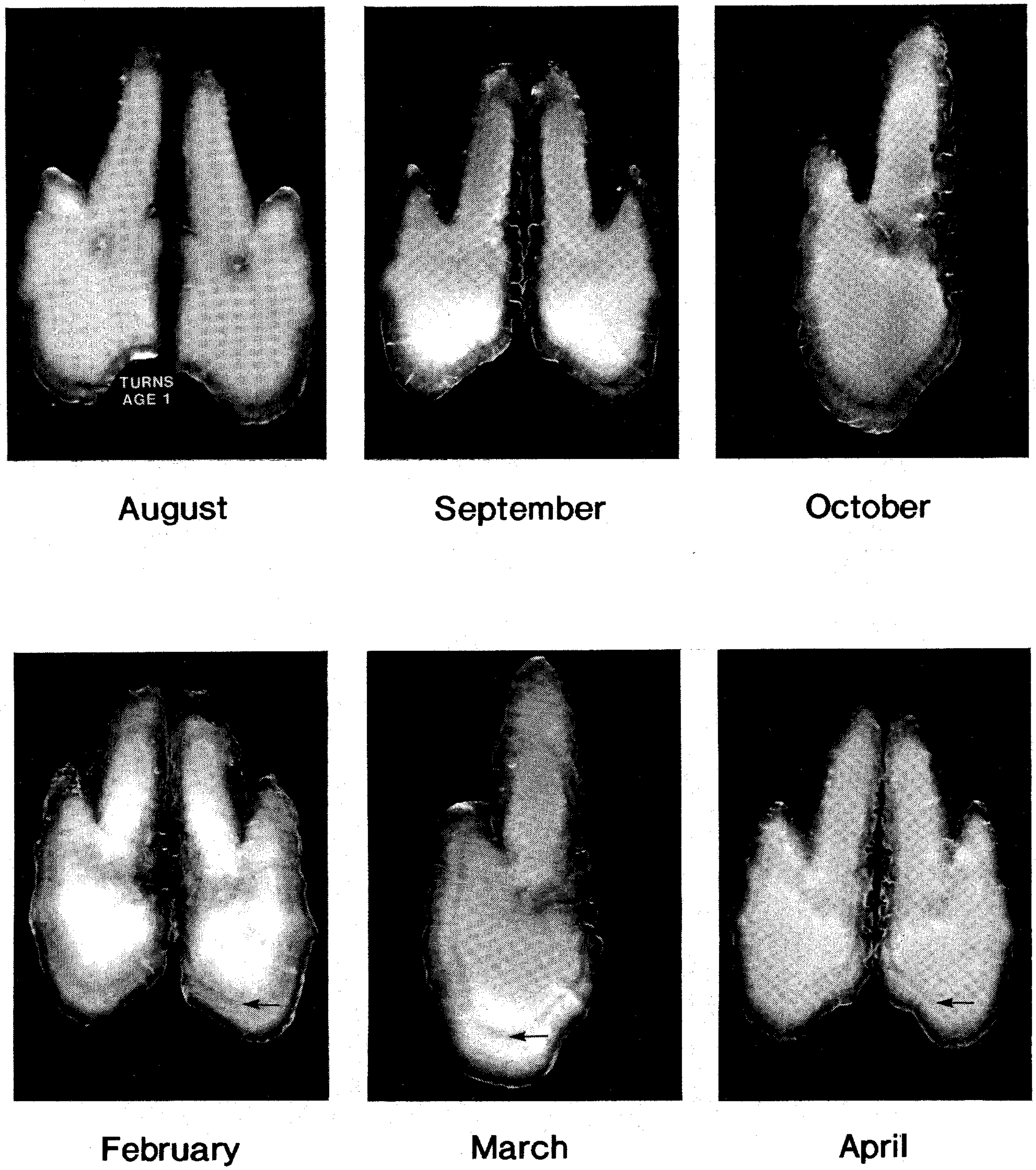
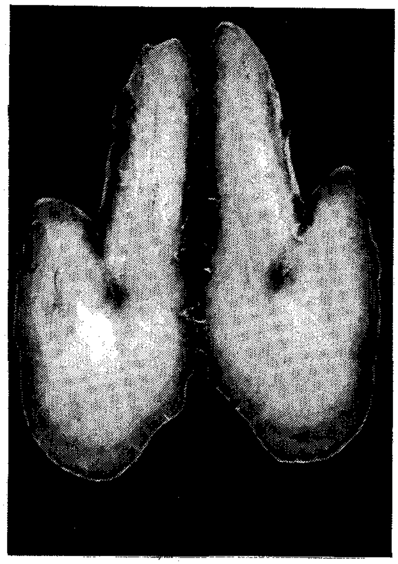
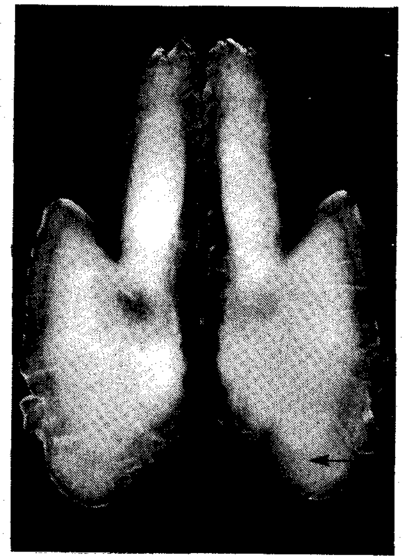


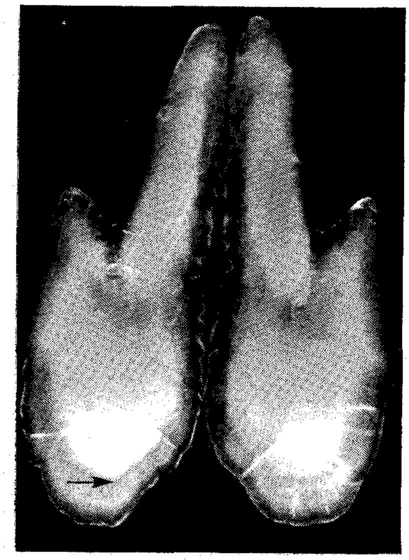
Figure 6. The change in the condition of the margin is traced for fish of the 1991 year class. In August of 1992, typical age one sardine otoliths display one complete annulus and a thin opaque margin, which grows in width through November. Around December of 1992, the beginnings of a translucent margin are apparent.



November

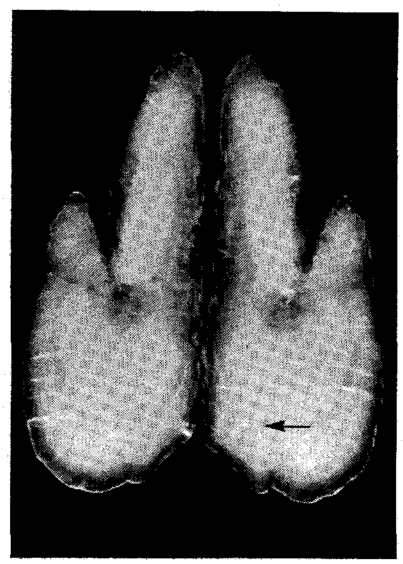


December

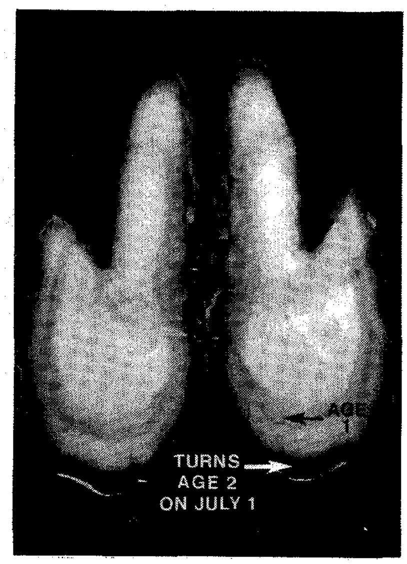


January

May



June



July

This translucent increment is widened through June of 1993, at which time the faint beginnings of an opaque deposition begin. On July 1, 1993, the fish of year class 1991 attain their second birthday, and a thin opaque zone marking their third summer of life is visible at the margin for most specimens.

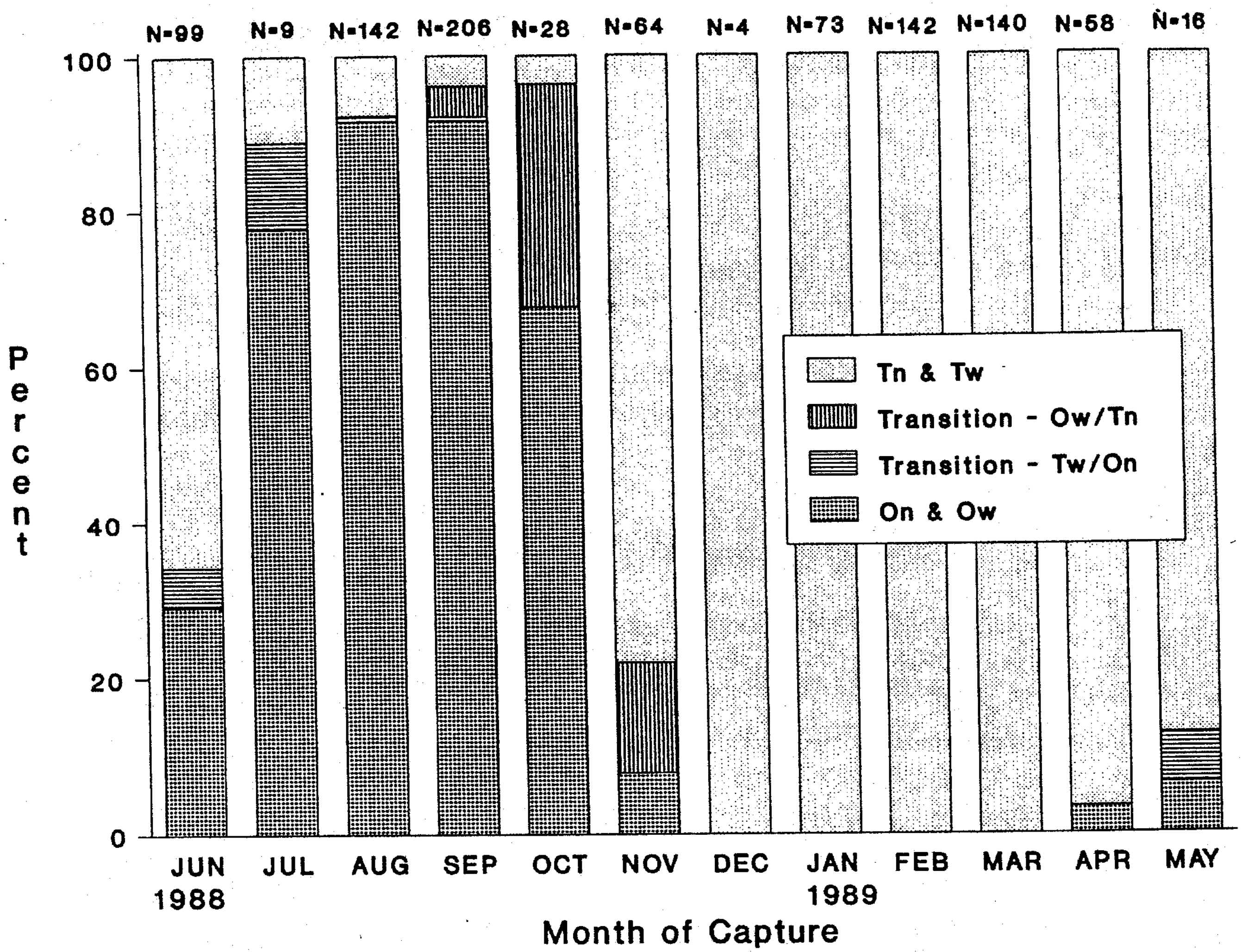


Figure 7. Seasonal changes in the otolith outer margin of age 2 (1986 year class) sardines (transposed from Barnes and Foreman, 1994).

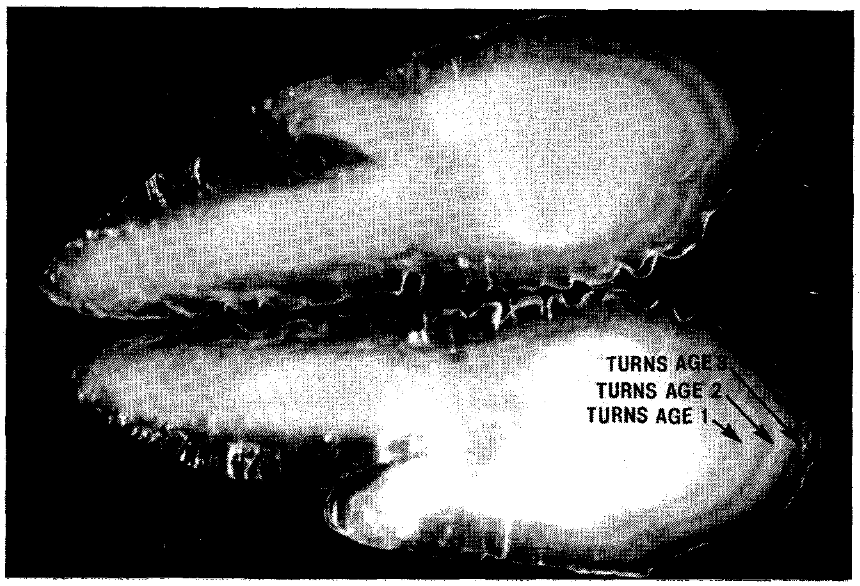


Figure 10. An otolith pair from a fish of age three, taken in the first quarter of 1995. Notice that the first opaque deposition becomes thinned and less pronounced as the first translucent increment becomes apparent. Inexperienced readers often mistake this transitory mark as an annulus, since it is compatible with the spacing of successive annuli.

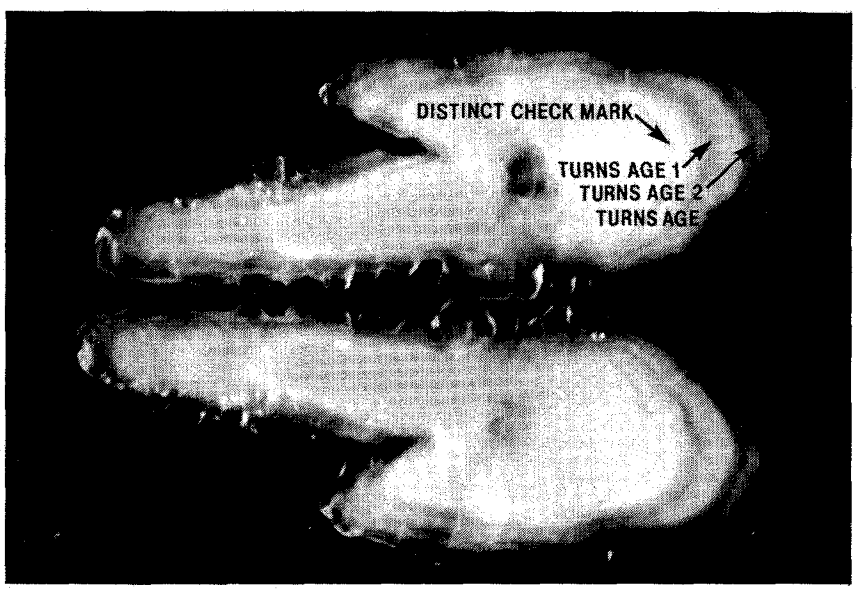


Figure 11. This otolith pair displays a very prominent check within its first summer's opaque deposition. Captured in the first quarter of 1995, this fishes age is determined as three. Although the spacing of this translucent mark would lead an inexperienced reader to believe it is an annulus, it is interpreted as a check because the following opaque deposition is of the same density as that toward the focus. The mark is also not as wide as the translucent increments that occur distally.

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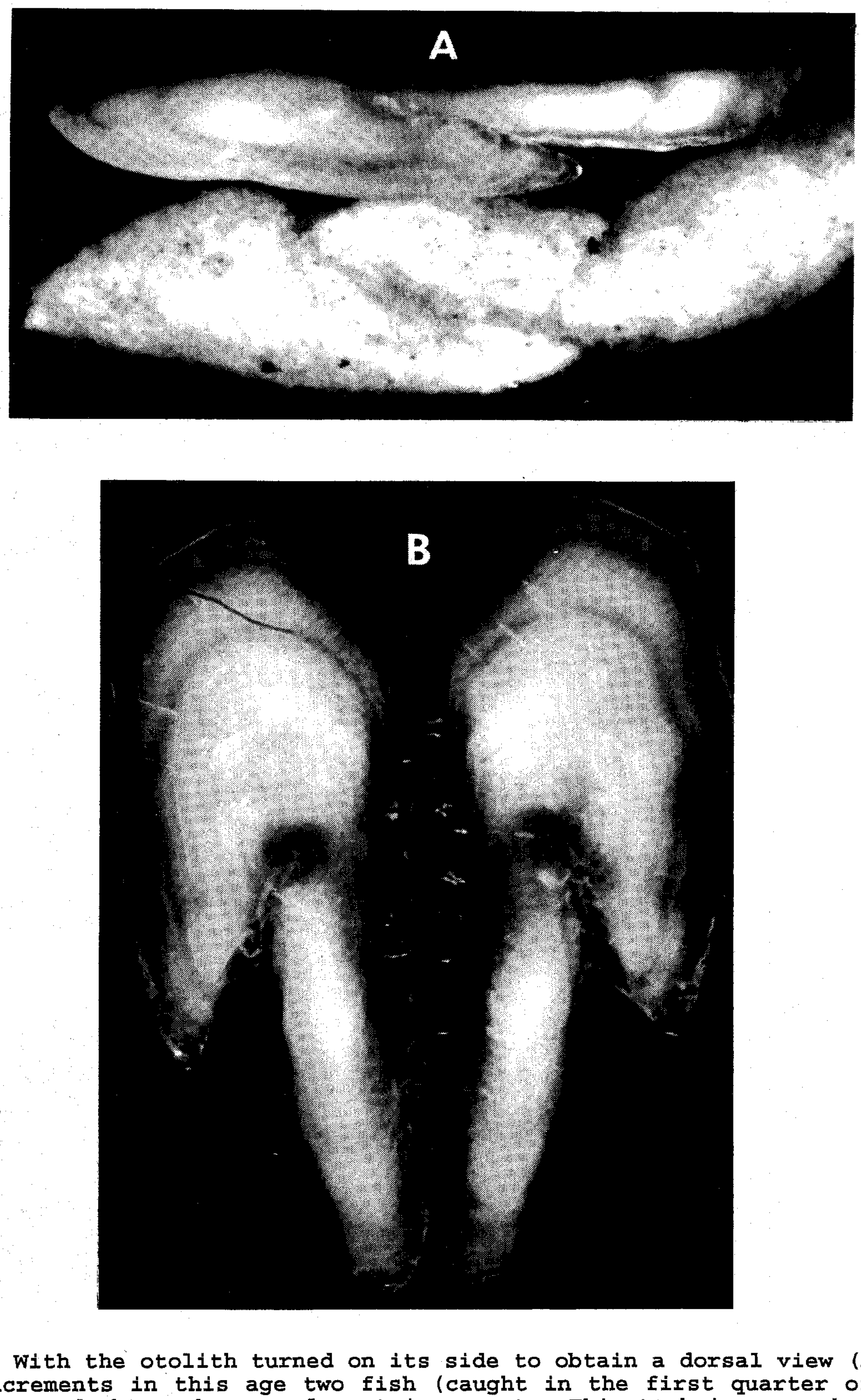

Figure 8. With the otolith turned on its side to obtain a dorsal view (A), the opaque increments in this age two fish (caught in the first quarter of 1995) appear elevated above the translucent increments. This technique can be useful when distinguishing true annuli from checks. The traditional exterior view is also shown (B).

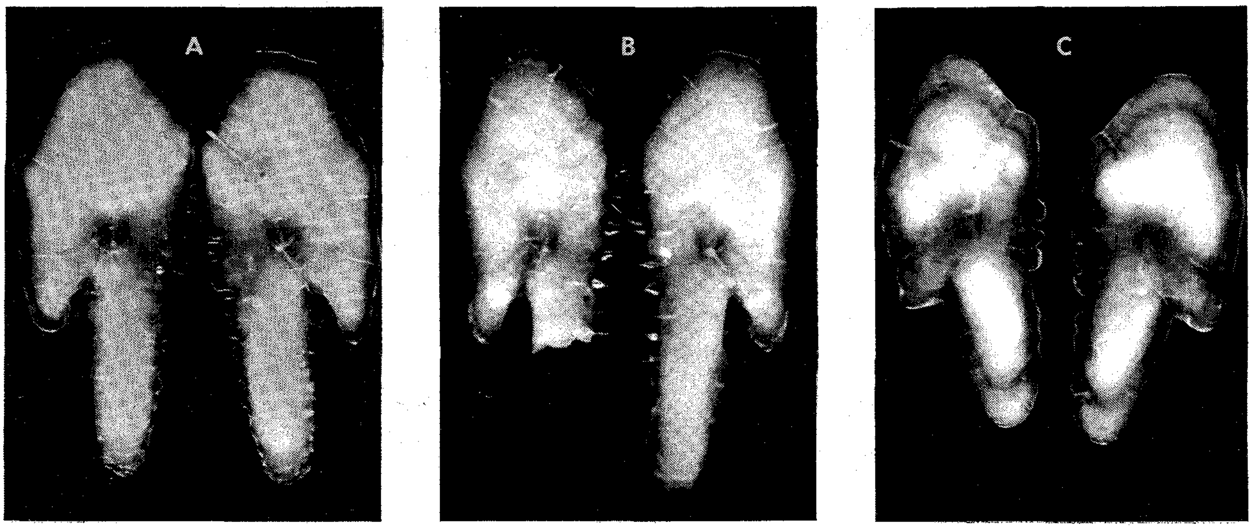

Figure 9. All these fish were captured in the first quarter of 1995, and are all members of the 1994 year class (age zero), despite extremely different appearances.

(A) These otoliths demonstrate the typical pattern one would expect of a fish captured in the first quarter of 1995, as there is a distinct opaque increment followed by a translucent margin the incomplete increment representing the current winter's growth.

(B) This first summer's opaque increment in this fish does not distinctly end, but rather simply "fades" into the translucent zone.

(C) Despite being caught in February, this pair displays a rare opaque-wide margin, which follows a translucent zone that could be interpreted as an annulus. This pattern is what you would expect to see in a fish landed in the fall. This otolith can be interpreted in two ways, although one explanation is more plausible than the other. Either this fish was hatched in July of 1994 and quickly deposited a complete opaque and translucent increment and had begun yet another opaque deposition prematurely when caught (as is common in younger fish), or the fish was spawned in July of 1993 and deposited a complete opaque and a complete translucent increment, and began another opaque deposition in July of 1994 that was still ongoing at the time of capture. The second option is less likely, because the second opaque deposition does not appear wide enough to represent approximately eight months (July 1994 to Feb. 1995) of rapid growth.

(D) The translucent increment in this fish is very wide and clouded, which could easily be misinterpreted. In many sample sets, the translucent increments are grayish instead of clear, making it difficult to discern where the opaque increments begin and end.

(E) Although captured in winter, there is no sign of a translucent margin on this otolith, reflecting continued rapid first-year growth.

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