

Revisiting daily age determination in juvenile anchoveta *Engraulis ringens*

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Abstract. Recent studies using otolith microstructure analysis have suggested that the duration of the juvenile stage in anchoveta (*Engraulis ringens*) is shorter than previously suspected, which suggests that the ages being entered into the traditional age-based stock assessment are incorrect. However, the interpretation of young pelagic fish otoliths remains problematic. To clarify the age interpretation of larval and juvenile *E. ringens*, newly hatched larvae were reared in a quasi-natural environment for periods of up to 103 days. The sagittal otoliths were subsequently examined and measured by international otolith experts in a double-blind workshop study. The young anchovy could be aged both accurately and precisely using otolith microstructure, after measures were taken to correct for unresolvable increments formed immediately after hatch. The presence of a fast-growth transition zone characterised by either considerable splitting or subdaily increments or both was confirmed. This study confirms the hypothesis of rapid growth and young age through the juvenile stage for anchoveta, suggesting that a critical appraisal of the annual age determinations used as the basis for anchoveta stock assessment is warranted. The otolith interpretation principles outlined in this study may apply broadly across many small pelagic fish species.

Additional keywords: Engraulid, splitting rings, validation.

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Introduction

In temperate ecosystems, anchovies (*Engraulis* spp.) are short-lived, small pelagic fishes, with a maximum life span ranging from 4 to 5 years and a maximum asymptotic length ranging from 16 to 19 cm (Iversen *et al.* 1993; Khemiri *et al.* 2007; Uriarte *et al.* 2016). Recent studies using otolith microstructure analysis have suggested that the duration of the juvenile stage is shorter and daily growth rates are faster than previously recognised in some species (La Mesa *et al.* 2009; Aldanondo *et al.* 2011; Cerna and Plaza 2016), including the commercially important anchoveta (*Engraulis ringens*) in the Humbolt Current system of the South Pacific (Pikitch *et al.* 2012). Under a ‘fast-growth’ scenario, anchoveta would reach their asymptotic length much more quickly than previously believed, and the time required to reach sexual maturity would be reduced to half (i.e. ~12 cm at ~180 days). This scenario implies that traditional age-based stock assessment methods, which depend upon age-structured catches of the previous years, would produce

inaccurate estimates of both current biomass and predicted total allowable catch (TAC; Cerna and Plaza 2016). However, the ‘fast growing and young age’ hypothesis based on otolith microstructure is still controversial due to the possible existence of double or triple subdaily growth increments in the juvenile region of the otolith in some anchovy species (Cermeño *et al.* 2006, 2008; Arneri *et al.* 2011).

To address the problematic interpretation of primary growth increments, Cermeño *et al.* (2008) compared two interpretation criteria for otolith growth increments in *Engraulis encrasicolus* in the Bay of Biscay: individual mark reading (IMR) and group band reading (GBR). Under the IMR interpretation, each growth increment was considered to have formed daily regardless of its appearance, whereas in the GBR interpretation each set of closely linked growth increments was considered to make up a daily increment. Cermeño *et al.* (2008) concluded that the GBR was the more reliable criterion as an ageing procedure for *E. encrasicolus*, but lacked wild known-age fish to test their

hypothesis. Conversely, Plaza and Cerna (2015) reported a closer correspondence between known daily age and the total number of increments when paired increments in a transition zone were counted separately in reared juvenile *E. ringens*. To resolve this ongoing controversy, and to develop criteria for correctly interpreting daily growth increments in sagittal otoliths of juvenile *E. ringens*, an international laboratory-based workshop of scientists with experience in otolith microstructure analysis conducted a double-blind exercise on 9–12 December 2017 in Valparaiso, Chile. The results of this workshop were based on known-age fish reared under quasi-natural conditions, with this basis separating the present study from all other published studies of anchovy age determination.

Materials and methods

Laboratory and field samples

Known-age larval and juvenile anchoveta *E. ringens* were reared from hatch in an outdoor quasi-natural seawater ‘pond’ enriched with nitrates and phosphates to better mimic the natural environment (Plaza and Cerna 2015). Newly hatched larvae were left in this system without additional management and sampling. At Day 52 after hatching, surviving juveniles were transferred to a rearing tank, where water temperature ranged from 14 to 18°C (mean \pm s.d., 15.9 \pm 0.7°C). Juveniles were fed twice daily with fractionated pellets (5812 Biomarine 2 mm; www.biomar.com, accessed 17 December 2018) designed for marine fish. Fish were periodically sampled from the juvenile rearing tank, and otoliths were removed from the sampled fish. Sagittal otoliths were prepared for otolith microstructure examination following the slide-glass embed method (Plaza et al. 2005).

Review of known age juvenile otoliths

A subsample of 13 prepared otoliths from the rearing study was examined at the workshop. All samples were blind labelled; thus, the true age of the fish was unknown to workshop participants at the time of ageing. Each of 13 the otoliths was independently examined and aged only once by all 9 workshop participants, both under a compound microscope (Axio Lab1; ZEISS; www.zeiss.com, accessed 17 December 2018), at magnifications from 400 \times to 1000 \times , and from digital images, with no discussion or comparison of interpretations until completion of the age determinations. A distinct check was formed on the date of transfer of the fish from the pond to the rearing tank at Day 52; therefore, all workshop participants recorded the age from what was presumed to be the hatch check to the transfer check (Zones A+B), and then again from the transfer check to the edge of the otolith (Zone C; Fig. 1). Zone A was defined as the region from the hatch check to the beginning of a transition zone interpreted as either broad and split or narrow and numerous growth increments, whereas Zone B was defined as the transition zone. Ages were not determined for Zones A and B separately. Age determination accuracy and bias was evaluated through comparison with the known age of each otolith, whereas ageing precision was measured with the index of the average percentage error (IAPE; Beamish and Fournier 1981) and the CV (Chang 1982).

The relationship between the known age after hatching and the number of increments formed until the date when fish were killed was determined using linear mixed models (LMM), with

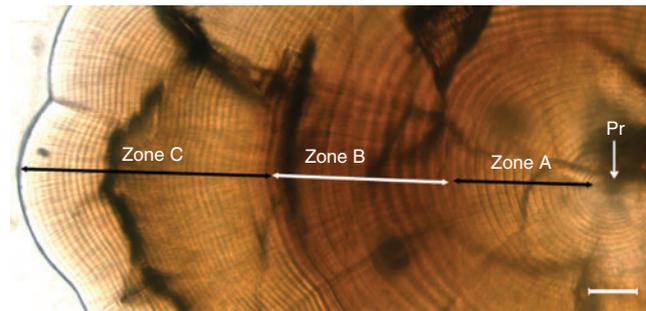


Fig. 1. Photograph of a sagittal otolith of a juvenile *Engraulis ringens* of 4.5-cm total length, illustrating the three characteristic microstructural zones. Zones A and B were formed while the specimen was maintained in an artificial feeding system with nutrients that mimicked the natural conditions. Zone C was formed once the specimen was transferred to an artificial feed system. P, primordium. Scale bar: 15 μ m. Image reproduced from Plaza and Cerna (2015).

the number of increments formed after hatching as the dependent variable, the total age as a main effect and the workshop participants as a random effect. Similarly, a LMM was used to examine the relationship between increment number and known age after the transfer check. Student's *t*-test was used to test whether the slope was significantly different from 1.

Results and discussion

Age determination in Zone C

The age estimates for Zone C (the outer region) were analysed first because this zone was considered easily interpreted. A graph of elapsed time *v.* increment count suggested that the daily growth increments were interpreted accurately (on average) over a post-check period of 16–51 days, with no appreciable bias and moderate precision (Fig. 2a; mean CV = 6.4%; IAPE = 4.6%). A LMM was used in a more rigorous test, with the number of increments after the otolith's natural tag as the dependent variable, the known age after transference from the pond to the rearing tank as the independent variable and the workshop participants as a random effect. The model was significant, the intercept was not significantly different than 0 (Table 1) and the slope was not significantly different from 1 (*t*-test, $t_{1,115} = 1.91 < t_{\alpha/2} = 1.98$). Nor were any of the random effects significant (Table 1). These results demonstrate that anchovy larvae form a continuous series of daily growth increments through at least a portion of the juvenile stage, and that these increments were interpreted correctly by the workshop participants.

Age determination in Zones A+B and total age

None of the workshop participants correctly estimated the known stage duration of Zones A+B, which was 52 days. On average, the mean (\pm s.d.) daily increment count through Zones A+B was 42.5 \pm 2.2 (range 38–45 days), which underestimated the true age by \sim 10 days (Fig. 2b; CV = 9.4%; IAPE = 7.0%). Similarly, none of the participants accurately estimated the total age of the juveniles, underestimating by an average of 10 days (Fig. 2b). Overall ageing precision was slightly better because of the better-defined Zone C increments; the mean CV of the total

Table 1. Summary statistics from a linear mixed model (LMM) to evaluate the relationship between the number of growth increments (dependent variable), the known age of the juvenile *Engraulis ringens* (independent variable) and the workshop age readers (shown as two-letter abbreviations) as a random effect

Separate LMM models were fitted for Zone C, when specimens were transferred to an artificial feeding system, and for Zones A+B+C, with total age spanning from hatching to the sacrifice date of juveniles. CL, confidence limit

| Zones | Effects | Estimates | Coefficient | s.e. | d.f. | <i>t</i> | Lower CL | Upper CL | <i>P</i> -value |
|-------------|---------|-----------|-------------|------|-------|----------|----------|----------|-----------------|
| Zone C | Fixed | Intercept | 0.66 | 0.53 | 8 | 1.24 | -0.40 | 1.71 | 0.25 |
| | | Known age | 0.97 | 0.02 | 107 | 59.51 | 0.94 | 1.00 | <0.001 |
| | Random | AH | 0.05 | 0.39 | 107 | 0.13 | -0.72 | 0.82 | 0.90 |
| | | AT | -0.63 | 0.39 | 107 | -1.63 | -1.40 | 0.14 | 0.11 |
| | | CR | -0.05 | 0.39 | 107 | -0.14 | -0.82 | 0.71 | 0.89 |
| | | FC | -0.16 | 0.39 | 107 | -0.41 | -0.93 | 0.61 | 0.68 |
| | | GM | 0.05 | 0.39 | 107 | 0.13 | -0.72 | 0.82 | 0.90 |
| | | GP | 0.19 | 0.39 | 107 | 0.49 | -0.58 | 0.96 | 0.63 |
| | | JC | -0.05 | 0.39 | 107 | -0.14 | -0.82 | 0.71 | 0.89 |
| | | MG | -0.05 | 0.39 | 107 | -0.14 | -0.82 | 0.71 | 0.89 |
| SC | 0.66 | 0.39 | 107 | 1.71 | -0.11 | 1.43 | 0.09 | | |
| Zones A+B+C | Fixed | Intercept | -5.98 | 2.95 | 8 | -2.03 | -11.83 | -0.13 | 0.08 |
| | | Known age | 0.95 | 0.03 | 107 | 27.96 | 0.86 | 1.02 | <0.001 |
| | Random | AH | 2.08 | 1.41 | 107 | 1.50 | -0.71 | 4.88 | 0.14 |
| | | AT | 0.11 | 1.41 | 107 | 0.08 | -2.68 | 2.90 | 0.94 |
| | | CR | 2.42 | 1.41 | 107 | 1.72 | -0.38 | 5.21 | 0.09 |
| | | FC | -2.85 | 1.41 | 107 | -2.03 | -5.64 | -0.06 | 0.05 |
| | | GM | 0.28 | 1.41 | 107 | 0.20 | -2.51 | 3.07 | 0.84 |
| | | GP | 1.88 | 1.41 | 107 | 1.34 | -0.91 | 4.68 | 0.18 |
| | | JC | -5.25 | 1.41 | 107 | -3.73 | -8.04 | -2.46 | <0.001 |
| | | MG | -1.52 | 1.41 | 107 | -1.08 | -4.31 | 1.27 | 0.28 |
| SC | 2.85 | 1.41 | 107 | 2.02 | 0.06 | 5.64 | 0.05 | | |

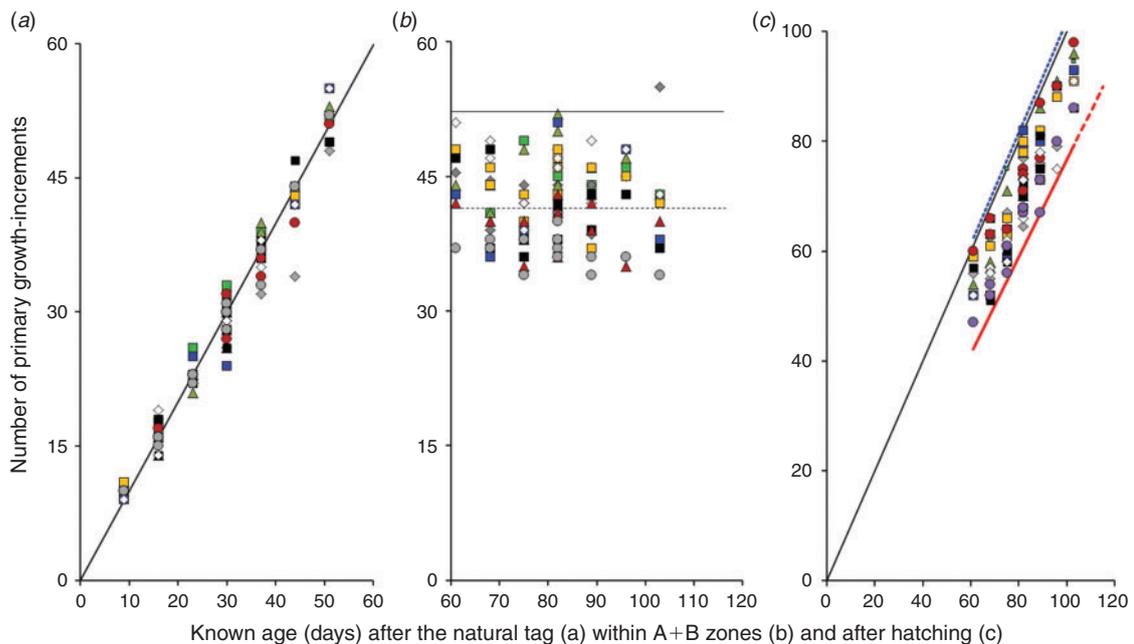


Fig. 2. Relationships between known age and increment number of otoliths from reared juvenile *Engraulis ringens*, counted by nine workshop participants. (a) Relationship between the known-age after the formation of the transfer check and increment count (Zone C). (b) Number of increments visible in Zones A and B in the otoliths of known-age juveniles. The mean count (dashed lower line) was 42; the actual duration was 52 days (upper continuous line). (c) Upper and lower 95% confidence limits (dotted and dashed lines) for increment count as predicted by a linear mixed model. The 1 : 1 line is shown as a solid line in panels (a) and (c). Scale bar: 5 μ m.

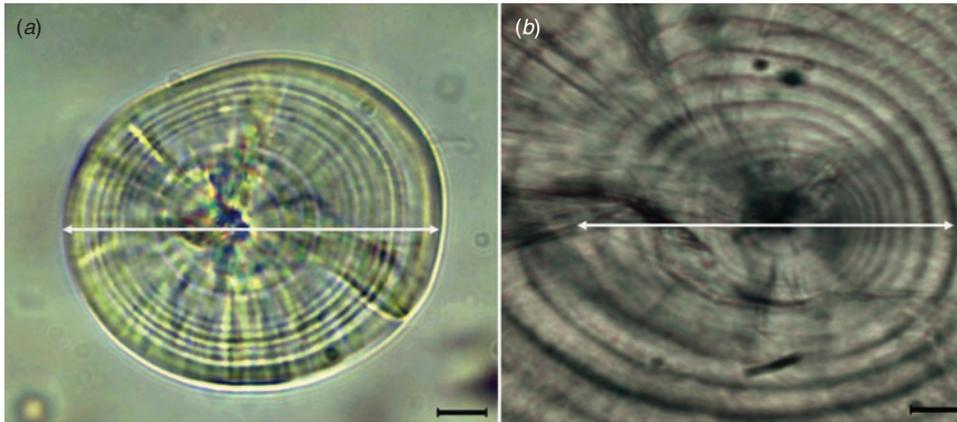


Fig. 3. Otoliths of (a) a known-age (15-day-old) larva and (b) a juvenile *Engraulis ringens*. (a) Fifteen daily growth increments are seen in the otolith from the 15-day-old larva. (b) The otolith of the juvenile is annotated with a line of the same length as the diameter of the larval otolith on the left. Fewer increments are visible within the marked diameter, even though they must be present. Scale bars: 5 μm .

increment counts (Zones A+B+C) across all workshop participants and otoliths was 6.3% (IAPE = 4.9%). The LMM was significant (Table 1; $P < 0.001$), with a slope (0.95) not significantly different from 1 (t -test, $t_{1,115} = 1.14 < t_{\alpha/2} = 1.98$), but the 95% confidence interval (CI) of the intercept did not include zero (mean of -6.0). Most of the age readers (random effects) were not significant (Table 1; t -test, $P < 0.001$). The combination of a negative intercept (indicating age underestimation) and a slope of < 1 (indicating additional age underestimation) in the LMM shows that increment count underestimated total age by ~ 11 days in a 100-day-old juvenile. The 95% CI of the LMM predictions (barely) included the known age (Fig. 2c), although the 90% CI did not.

Missing increments around the core

To determine whether there were unseen increments around the otolith core, increment counts at a fixed otolith radius were compared between larval and juvenile anchovy otoliths. Known-age (15-day-old) anchovy larva otoliths, coming from a parallel experiment, were very small and thin, and required no polishing to reveal 14–15 daily increments at an average otolith radius of 24.73 μm (Fig. 3a). However, when this same otolith radius was overlaid on the much-thicker (despite polishing) known-age juvenile anchovy otoliths, only five to eight increments were visible (Fig. 3b). Thus, some increments became unresolvable in the juvenile otoliths.

Estimation of missing growth increments around the core

Otolith radius (OR) increased exponentially with daily age of larvae ($\text{OR} = 6.79 \times \exp(0.08 \times \text{age})^{-1}$; $F = 3204$; $P < 0.001$; $R^2 = 0.96$). To estimate the number of daily increments theoretically present around the core in an otolith of a given radius, the same data were natural log transformed and refitted to predict age, as follows:

$$\text{Age} = 11.5 \times \ln(\text{OR}) - 21.4$$

where $F = 3204$; $P < 0.001$ and $R^2 = 0.94$ (Fig. 4).

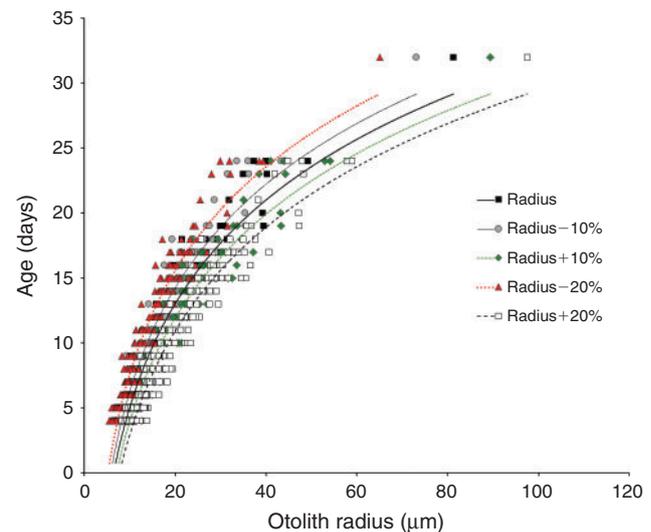


Fig. 4. Sensitivity analysis of the relationship between otolith radius and age in *Engraulis ringens* larvae as a function of variable otolith growth rates. The differently dotted lines represent simulated variations in growth rates around the original exponential curve, represented by the solid black line.

Entering the OR of the innermost visible increment as the independent variable into the above equation yielded estimates of 7–15 unresolved increments in the workshop otoliths (Table 2). Once the number of unresolved increments was added to the observed increment number, total estimated ages were not significantly different (± 3.5 days) from the known ages of 68–103 days (Table 2; t -test, $P = 0.94$).

The steepness of the otolith–age exponential regression is a reflection of growth rate, and thus affects the predicted number of unresolved increments within a given OR. Slower growth would produce a larger number of unresolved increments. The growth rate of the known-age anchovy larvae was very similar to that measured in wild fish (Contreras et al. 2017), suggesting that the fitted curve is broadly appropriate in both reared and

Table 2. Illustration of the daily age correction in five known-age juveniles of *Engraulis ringens*

Age was determined based on increment counts through direct observation under a light microscope, as well as from digital images of the same otolith. The number of unresolved increments estimated to have been present before the first visible increment (from Fig. 3b) is also shown, as is the total resulting estimated age

| Known age of juvenile (days) | Direct age determination (days) | Image-based age determination (days) | Estimated number of missing increments | Corrected estimated age (days) |
|------------------------------|---------------------------------|--------------------------------------|--|--------------------------------|
| 68 | 66 | 64 | 7.5 | 71.5 |
| 75 | 64 | 62 | 11.0 | 73.0 |
| 82 | 74 | 70 | 9.5 | 79.5 |
| 89 | 84 | 80 | 7.5 | 87.5 |
| 103 | 90 | 91 | 15.0 | 106.0 |

wild fish. However, growth rate variations across years are inevitable. Sensitivity analyses demonstrated that a $\pm 20\%$ variation in growth rate resulted in ± 3 days difference in the estimated number of unresolved increments for a given otolith (Fig. 4), indicating that the adjustment for unresolved increments was not particularly sensitive to growth rate.

Sources of age underestimation

The close correspondence between the number of days after natural tag formation and the number of observed post-tag growth increments is clear evidence of a daily periodicity of otolith growth increment formation during the juvenile stage of this species, which matches the results of Plaza and Cerna (2015). However, some explanation is needed of the asynchrony between the total known age and the total number of growth increments in the juveniles. The first and most reasonable explanation is that the transition zone was interpreted incorrectly; indeed, all workshop participants interpreted the transition zone as consisting of broad, split increments (e.g. GBR; Cermeño *et al.* 2008). If the 'subdaily' increments in the transition zone were interpreted as daily (e.g. IMR; Cermeño *et al.* 2008), overall age estimates increased by ~ 13 days. Key to this scenario is that the IMR-interpreted age only corresponds with the actual age if it is assumed that the daily increments first start to form 3 days after hatch (as reported by Hernández and Castro 2000), and that all larval daily increments can be seen in older fish. The following paragraphs demonstrate that this assumption is not warranted, and thus the IMR approach is not valid in anchovy.

Missing rings around the core and occurrence of a second check

In many small pelagic fish species, daily increments appear not to form until well after hatch; for example, in known-age herring (*Clupea harengus*) larvae, increment deposition rates of < 1 day are always observed, particularly in larvae growing less than 0.4 mm day^{-1} (Geffen 1982; Folkvord *et al.* 2000; Feet *et al.* 2002). Given that there was no physiological explanation for the absence of daily increment formation in these species, the apparent anomaly remained until Campana *et al.* (1987) demonstrated that the observed rate of OR increase in larval herring otoliths would necessarily form increments with a width that

was less than the theoretical resolution limit of a light microscope. The number of unresolvable increments was exactly equal to the observed 15- to 20-day age underestimation, thus explaining the apparent anomaly. The age underestimation was exacerbated in larger otoliths because of the difficulty of polishing exactly to the midplane of the otolith. The results of the present study indicate that exactly the same phenomenon appears to apply to larval anchovy.

The core area in otoliths from most larval fishes is usually characterised by a central opaque primordium surrounded by a diffuse zone with no visible increments until the appearance of a prominent concentric hatch check (Campana and Neilson 1985; Campana 1992; Ding *et al.* 2015). Species with a prolonged embryonic period, such as salmonids, may form multiple increments medial to the hatch check (e.g. Radtke and Dean 1982; Moyano *et al.* 2012). Distal to the hatch check, clear and distinctive daily growth increments are formed in many species (Zhang and Runham 1992), whereas other species may form a sequence of very narrow growth increments, followed by either or both a second prominent check or an abrupt shift to wider distinctive increments (Islam *et al.* 2009; Leander *et al.* 2013). This latter pattern was observed in the present study in sagittae of reared juvenile *E. ringens*.

The existence of a second check distal to the hatch check, as previously observed in *E. ringens*, has been linked to the shift from endogenous to exogenous feeding after yolk sac absorption in demersal fishes, and to the extrusion of live larvae in the case of viviparous fishes, such as *Sebastes thompsoni* (Kokita and Omori 1998) and *Sebastes inermis* Plaza *et al.* 2001). In other studies of pelagic fish larvae, the first daily increment forms either immediately (Zhang and Runham 1992; Alemany and Alvarez 1994; Aldanondo *et al.* 2008) or a few days after hatching on the date of yolk sac depletion (Watanabe and Kuji 1991; Xie *et al.* 2005). Although Hernández and Castro (2000) reported that the first daily increment in anchoveta formed 3 days after hatching, narrow increments have been observed between the hatch check and the yolk-sac check in reared larvae of many pelagic species, such as *C. harengus* (Geffen 1982), *E. encrasicolus* (Palomera *et al.* 1988) and *Sardina pilchardus* (Alemany and Alvarez 1994). Indeed, Aldanondo *et al.* (2008) confirmed that the first daily increment was laid just after hatching in larval *E. encrasicolus*, after which up to four narrow daily increments were formed before yolk sac depletion.

This type of otolith growth pattern is expected to apply to the otolith core area of *E. ringens* as well.

Split growth increments in the otolith transition zone

The workshop review of known-age juvenile anchovy otoliths reared under quasi-natural conditions confirmed that young anchovy could be aged precisely using otolith microstructure, but that they could only be aged accurately after measures were taken to correct for bias due to unresolved increments close to the core. These corrective measures (the equation describing larval age as a function of OR) are readily defined for any new species, but the parameters of the equation are almost certainly species specific. In addition, the present study suggests the presence of a fast-growth transition zone in juvenile anchoveta otoliths characterised by either considerable splitting or sub-daily increments or both. Such an interpretation is consistent with the GBR interpretation proposed by Cermeño et al. (2006, 2008) for *E. encrasicolus* in the Cantabric Sea, rejects the IMR criteria for counting every individual increment in the transition zone and is fully consistent with widespread criteria for reading and interpreting daily growth increments in many other species (Campana 1992). Finally, and perhaps most importantly, the present study confirms the hypothesis of rapid growth and young age for this species in the Humboldt Current system, which casts doubt on the accuracy of existing yearly age determinations. A critical appraisal of the annual age determinations used as the basis for anchoveta stock assessment appears warranted.

Conclusion

We anticipate that the otolith interpretation principles outlined here can be applied broadly across many small pelagic fish species from temperate waters, most of which have been considered to grow slowly during their first week or two of life. Failure to correct for unresolvable increments formed after hatch, and the presence of sub-daily increments in the juvenile transition zone, could introduce serious age-specific error into any daily age assignment.

Conflicts of interest

The authors declare that they have no conflicts of interest.

Declaration of funding

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