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Testing assumptions underlying cabezon (*Scorpaenichthys marmoratus*) otolith microstructure analysis using wild-caught juveniles and opportunistic rearing of eggs and larvae

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Funding Statement

Multiple funding sources supported this project including Hatfield Marine Science Center and Oregon Sea Grant awards to M.W. S.S. was supported during this study and its preparation for publication by National Science Foundation grant OCE 2125407; K.G.C. was supported by the Ocean Science Innovation Fund at Oregon State University. This study was supported in-kind by ODFW and the Oregon Coast Aquarium.

Abstract

Otolith microstructure analysis provides critical biological and ecological information about the early life history of fishes. This information is particularly important to interpret and predict population dynamics for socio-economically important fisheries species; however, several key assumptions underpin the use of otolith techniques. We validated the use of this analysis for cabezon (*Scorpaenichthys marmoratus*; Ayres, 1854), a long-lived, large-bodied cottid constituent of nearshore fisheries from Baja California, Mexico to Alaska, USA. To test three critical assumptions, we coupled otolith and morphometric analyses from an opportunistic rearing study of cabezon eggs and larvae with a long-term time-series of juvenile cabezon field collections. We confirmed daily otolith increment deposition in laboratory-reared larvae, identified the timing of first otolith increment deposition, and examined the relationship between otolith growth and somatic growth in field collected juveniles, validating the use of otolith microstructure analysis in biological and ecological interpretations of early life history traits for this species. Our findings also indicated that the absorption of yolk sac reserves, and likely the transition to exogenous feeding, play an important role in regulating otolith increment deposition. Finally, we found within-brood size-at-age variation, which may be an advantage for young fish in prey-limited environments.

Keywords

Larval fish, otolith microstructure, rearing, recruitment, settlement-stage, validation

Introduction

Most marine taxa have a biphasic life cycle whereby benthic adults spawn pelagic eggs and larvae that remain in the plankton for weeks to months before returning to settle in adult habitat. Marine fishes experience upwards of 99% mortality during these sensitive early life stages (Peterson and Bradford, 1987), so factors that affect growth and survival through these early stages have a disproportionately large effect on adult population dynamics. For this reason, it is important to understand the spectrum of variation that exists in early life history traits and how these traits may confer survival advantages.

Growth and survival of the early stages of marine fishes are highly correlated with temperature, feeding success, and other environmental factors, thus it is difficult to examine early life history traits using morphometric measures alone. Fortunately, all bony fishes have otoliths, calcium carbonate ear stones that aid in orientation, hearing, and balance, and simultaneously provide valuable data on age and growth. For many species, major life history transitions such as hatching, first feeding, and metamorphosis are recorded in otolith microstructure, and otolith growth is often proportional to somatic growth (Campana, 1990). Therefore, measurement of several early life history traits is often possible using otoliths, providing key insights into the factors that affect growth and survival in early life (Sponaugle, 2009).

To substantiate biological and ecological inference from otolith microstructure, several key assumptions should be tested (Geffen, 1992): (1) deposition of material is a reliable chronological record at the time scale of interest (i.e. daily), (2) the timing of first increment deposition is known (and is ideally associated with a known biological process such as hatching or the transition from endogenous to exogenous feeding), and (3) otolith growth has a consistent relationship with somatic growth (Thorrold and Hare, 2002). However, some of these assumptions can be challenging to validate without laboratory rearing.

Cabezon (*Scorpaenichthys marmoratus*; Ayres, 1854) is one such species where otoliths can provide critical early life history information. Cabezon is a socio-economically important species in commercial and recreational fisheries throughout its range, but the patterns and processes driving adult population dynamics are not well understood. What is more, almost nothing is known about patterns of population replenishment, or recruitment (but see Ottmann et al., 2018). For this reason, there is interest in examining otolith microstructure in larval and juvenile cabezon to identify early life history traits that may be important determinants of recruitment strength.

As a long-lived, large-bodied member of the Cottidae family that inhabits nearshore waters from Baja California, Mexico, to Alaska, USA (Quast, 1968; Miller and Lea, 1972; Love et al., 2005), cabezon lay demersal egg masses in the recesses of natural and man-made reefs, with males demonstrating nest guarding behavior (Garrison and Miller, 1982). The presence of larvae in ichthyoplankton surveys and variation in ovary condition indicate that the timing and duration of spawning varies by latitude and with environmental conditions. In Washington and Oregon, spawning lasts several months and peaks in March and April (Lauth, 1988; Hannah et

al., 2009). Fertilized eggs incubate for 25-49d (average 34d; Feder et al., 1974). Newly hatched larvae range from 4.4-6.5mm and flexion occurs around 7.5-8.7mm (Materese et al., 1989). Larvae metamorphose into pelagic juveniles at around 14mm standard length (L_s), and remain pelagic until at least 35mm L_s, but pelagic juveniles as large as 60mm L_s have been observed (Ottmann et al., 2018). The pelagic larval and juvenile periods last approximately 3-4mo (O'Connell, 1953). Larvae and pelagic juveniles are heavily pigmented, likely an adaptation to the extreme ultraviolet radiation characteristic of the neuston (top 10-20cm of the ocean), which serves as a nursery ground for cabezon (Zaitsev, 1971; Richardson and Pearcy, 1977; Shenker, 1985; Doyle, 1992; Helm, 2021).

We undertook this study on cabezon to test the assumptions listed above, thus enabling further biological or ecological inference from otolith microstructure analysis. Specifically, our goals were to: 1) validate daily increment deposition in laboratory reared larvae, 2) identify the timing of first increment deposition, and 3) examine the relationship between otolith growth and somatic growth in field collected juveniles.

Methods

The care and use of experimental animals complied with Oregon, USA animal welfare laws, guidelines and policies as approved by the National Marine Fisheries Service (permit #18058) and the Oregon State University Animal Care and Use Protocol (permit #4183).

Egg collection and rearing conditions

A single brood of fertilized, eyed cabezon eggs was obtained from the Oregon Coast Aquarium, Newport, Oregon, USA (44.61765 N, -124.04725 W) in November, 2020 to be reared through hatching and subsampled for morphometric and otolith analysis. The brood was located in a closed-system exhibit at the aquarium held at 10.6˚C. Although the date of egg laying and fertilization are unknown, the brood was actively guarded by an adult female cabezon for at least three weeks prior to collection, consistent with known average incubation period (Feder et al., 1974). Several cabezon share the exhibit tank, so it is possible that the brood was fertilized by several males.

The brood was moved nearby to an isolated 90-liter tank at the Hatfield Marine Science Center, Newport, Oregon (44.62239 N, -124.04561 W) and reared in a closed system. Temperature was maintained by a water bath that received flow-through sea water from Yaquina Bay for the remainder of incubation and for 14d post hatching (dph). Water changes were performed each day of the incubation period and until 4dph. From 4dph to 14dph, water changes occurred every other day. The seawater in the tank was continuously oxygenated by air stones. The water temperature along the open coast adjacent to Yaquina Bay ranged from 9.7˚C – 12˚C (NOAA Station SBEO3 at South Beach, Oregon). No supplemental food was provided for the duration of the 14-d study, a condition that may be experienced by larvae that hatch in lower productivity waters. The indoor tank was not exposed to a controlled light regiment but received natural light from windows and additional light during water changes.

Subsamples of n=20 were collected during the incubation period (eggs), the day of hatching (larvae), 1-4dph, and 6, 8, 10, 12, and 14dph.

Field collection of juveniles

Juvenile cabezon were obtained from the Standard Monitoring Units for the Recruitment of Fishes (SMURF) Project that is a collaboration between Oregon State University, the Oregon Department of Fish and Wildlife Marine Reserves Program, the Oregon Coast Aquarium, members of the local fishing fleet, and community volunteers. The goal of this larger project is to monitor the seasonality and magnitude of the recruitment of nearshore groundfishes to the Oregon's nearshore waters. The SMURF project began in 2011 and is ongoing, with sampling in and around two of Oregon's marine reserves on the central and southern Oregon coast. Juvenile cabezon samples utilized in this study (n=296) were collected in and around Otter Rock Marine Reserve (44.73701-44.78369 N, -124.08135-124.07372 W) over five different years (2013, 2015, 2016, 2018, and 2019), spanning variable environmental conditions. Juvenile cabezon were collected from the SMURFs every two weeks during the summer settlement season, which starts in April-June (weather dependent) and extends into September (Love, 2011).

SMURFs were designed to sample settlement-stage juvenile fishes that are often found in kelp habitats immediately post-settlement. SMURF collectors consist of black polyvinyl chloride mesh folded inside a long (100 x 35 cm) cylinder of garden fencing, forming a 3-D structure that simulates natural settlement substrates such as a kelp canopy. These collectors provide an artificial refuge for settlement-size fishes high in the water column. SMURFs are deployed 1m below the surface by attaching them to a mooring anchored in sandy substrates in ~15m of water, 390-1,200m from shore. The deployment locations were selected at a minimum distance of 25 m offshore of underwater boulders and kelp canopy to ensure direct settlement of fish from the water column to SMURFs as opposed to their movement up to SMURFs from the surrounding habitat.

Morphometric measurements

All reared larvae except those 14dph were imaged live using a Leica DMLB microscope. Images were analyzed using ImagePro 9.0 software. A subsample of larvae (n=5) at each timepoint were imaged after preservation in 90% ethanol (EtOH) to calculate a shrinkage factor. Morphometric measurements were obtained for each live and preserved specimen (n=213) including notochord length (L_N), body depth, gut depth, and oil globule size (*sensu* Moser, 1996; S1). The shrinkage factor was applied to 14dph larvae to back-calculate live morphometrics. Juvenile cabezon L_s was measured to the nearest 0.1mm using digital calipers prior to preservation (n = 296).

Otolith analysis

All sagittal and lapillal otoliths were removed from the cranium of a subsample (n = 5) of reared larvae at each time point and placed in immersion oil on a microscope slide. The otoliths were imaged after at least 2d of oil immersion to aid with image clarity. Sagittal and lapillal otoliths were distinguished by size, shape, and position within the cranium, with the lapillus lateral and dorsal to the sagitta (Figure 1). All otoliths were measured, but only sagittal otoliths were used for further otolith microstructure analysis. The shape of the sagittal otoliths was roughly ovoid, but not always, thus consistent identification of the longest reading axis was difficult. To overcome this challenge, we measured all four axes and selected the longest on the minor (lateral) axis.

Saggital otoliths were removed from juvenile cabezon (n=296). The left or right otolith was randomly selected for otolith microstructure analysis. We embedded sagittal otoliths in Crystalbond thermoplastic resin (Electron Microscopy Science) and used lapping paper to polish otoliths along the sagittal plane. Juvenile cabezon sagittal otoliths are also ovoid and we measured the longest axis on the minor (lateral) axis.

Larval and juvenile otoliths were read at 400x using a Leica DMLB compound microscope equipped with polarized transmitted light, and increments were interpreted using image analysis software (ImagePro v.9.0). Following standard procedures (e.g., Sponaugle, 2009; Ottmann et al., 2019; Fennie et al., 2020), for larval cabezon, we identified the otolith core and hatch mark, enumerated otolith increments, and measured the width between neighboring otolith increments to estimate the age (number of increments between hatching and otolith radius), daily growth rate (increment widths), and size-at-age (otolith radius-at-age) for each individual. Similarly, for juvenile cabezon, we enumerated otolith increments and the maximum minor otolith radius to estimate the age and otolith size of each individual. Each otolith was read twice by the same reader without access to prior reads or sampling data. If the two reads differed by ≤5%, one read was randomly chosen for analysis. If reads differed by >5%, otoliths were read a third time. Otoliths where the three reads differed by >5% would be removed from analysis (n=0; Sponaugle et al. 2009)

Data visualization and analysis

All data analysis was performed in R Version 4.0.0 (R Core Team, 2020) and visualizations were carried out using the package ggplot2 (Wickham, 2016). We used linear modeling to quantify the shrinkage factor associated with preservation with EtOH and to investigate the relationship between juvenile cabezon otolith size, fish size, and age. Kruskal-Wallis tests, a non-parametric alternative to ANOVA, followed by post-hoc Wilcox tests were used to identify significant differences in size-at-age between groups of larvae of the same age. Due to a small sample size (n=5 per dph), the assumption of normally distributed data could not be met and thus a non-parametric test was an appropriate alternative.

Results

Morphometric measurements

Mean hatch length for reared cabezon larvae was 5.86mm L_N. Mean L_N increased from hatching until 4dph (mean maximum L_N at 4dph was 6.40mm), where it remained approximately constant for one day. From 6 to 14dph, mean L_N was variable, with the mean decreasing to 6.09mm (Figure 2a). Both body depth and gut depth decreased with age (Figures 2b-c). The L_N to body depth ratio increased (larvae became longer and skinnier) until 4dph (Figure 2d). From 6 to 14dph, the mean ratio was variable. The size of the oil globule was also measured in larvae where it was easily visible, but the number of such individuals was small and, as expected, diminished with age.

Morphometric measurements taken before and after preservation in 90% EtOH were used to calculate a shrinkage factor. The live L_N was significantly linearly related to the post-EtOH L_N ($p < 0.001$, $R^2 = 0.66$; S2). The relationships between live body depth and gut depth vs post-EtOH measurements were not significant ($p > 0.05$).

Otolith analysis

We identified the presence of pre-hatch embryonic increments. In general, two to five of these pre-hatch increments were present, though they were not consistently clear among individuals and across stages. Importantly, we confirmed that the first post-embryonic increment is associated with hatching. Interestingly, distance to the hatch mark was shorter in older larvae: individuals that survived longer had hatch marks positioned closer to the core (Figure 3c). For example, the average location of the hatch mark in 2dph was 18.23µm whereas in 14dph larvae the hatch mark occurred at 14.97µm.

From hatching until 6dph the number of increments enumerated in the otolith corresponded to the known age of the larvae. However, after 6dph the number of increments became decoupled from the known larval age (Figure 3a). For example, the mean total number of increments observed at 8 and 14dph was 5.7 and 8.0, respectively (Figure 3a). Despite inconsistent increment deposition in older individuals, the mean otolith radius increased with age (Figure 3b).

Otolith microstructure analysis of field collected juvenile cabezon revealed a significant linear relationship between fish size and age ($p < 0.001$), and between otolith size and age ($p < 0.001$). There was also a significant linear relationship between the residuals of fish size and age and otolith size and age ($p < 0.001$; Figure 4). Juvenile cabezon of 27.33 – 59.48mm L_s were 63-129d old, and their otolith radii ranged between 261.94 – 466.97µm.

<u>Abnormal otoliths</u>

In addition to the decoupling of known ages and otolith increment numbers in reared cabezon larvae that survived longer, there were several notable abnormalities that increased in occurrence in these older larvae. There was a high degree of asymmetry between the left and right otoliths (Figures 5a-b) and early formation of secondary growth primordia (Figure 5a). Finally, an abnormal banding pattern was observed in two 14dph individuals. The 'normal'

growth pattern (Figure 5c) consists of a clear hatch mark followed by several small increments, and the 'abnormal' growth pattern consists of an abnormally early hatch mark (at 12.29 and 13.58µm) followed by large (often twice the size of the increments in the normal growth pattern; Figure 5d). Both the normal and abnormal growth patterns were present in juvenile cabezon as well, with the abnormal growth pattern being relatively rare (in an anecdotal study of core regions, we found 7.92% abnormal in n=101 juveniles).

Growth and size trajectories

Mean size-at-age trajectories of reared larvae illustrate an emerging pattern where, on average, larvae that survived longer (i.e., collected at 14dph) were smaller-at-age than larvae that were collected at younger ages. Specifically, 14dph individuals were significantly smaller at ages 1-3d than 0, 2, and 4dph individuals and 14dph larvae were significantly smaller at age 4d than 4dph individuals ($p < 0.05$; Figure 6). Similarly, mean otolith growth trajectories suggest an emerging pattern of slower growth in larvae that survived longest (14dph; S3). These differences were not significant, likely due to a small sample size (n=5 otolith samples per time point).

Discussion

Our findings lay the groundwork for subsequent studies of the early life history stages of cabezon. Reared larvae in this study experienced unusual conditions including protracted starvation, abnormal photoperiod, and disturbance from water changes, which likely induced a high degree of stress that can complicate the interpretation of our findings. Despite these challenges, this work highlights the importance of opportunistic sampling and rearing, especially with the help of stakeholder partners, such as local aquariums.

The first ecological responses we documented were morphometric and otolith responses of reared larval cabezon to starvation. As expected, as larvae depleted resources from their yolk sacs, they grew longer and skinnier. Because no food was supplied, larvae were unable to transition to exogenous feeding and unable to sustain consistent growth. The ability of larvae to withstand starvation is region- and species-specific; larvae of several temperate fish species can withstand starvation for several days (McGurk, 1984; Koss & Bromage, 1990; Gisbert & Williot, 1997; Gisbert et al., 2004), while some tropical fish larvae can survive only a few hours (Houde, 1974). Our findings suggest that yolk sac depletion occurs at 4-6dph, as this is when larval notochords ceased to increase in length and known age and otolith-derived age (increment number) began to decouple. This observation demonstrates that not only are yolk sac absorption and exogenous feeding critical physiological mechanisms for survival, but also that they play a role in regulating daily otolith increment deposition.

Despite less-than-optimal rearing conditions, close examination of the cabezon larvae together with their otoliths enabled confirmation of key assumptions underlying biological and ecological inference from otolith microstructure analysis. Prior to yolk sac absorption, otolith increment deposition occurred daily. While starvation complications noted above caused

decoupling of the known age and otolith derived age in older larvae, based on similar studies in other fishes, it is highly likely that daily deposition continues after the transition to exogenous feeding. Because larvae experienced an inconsistent photoperiod and were still able to regularly deposit increments it is likely that photoperiod plays a minor role in regulating increment deposition, at least in comparison to feeding. Temperature is often implicated in the regulation of increment deposition (Tonkin et al., 2007) and was variable over the duration of larval rearing in this study (ranging from 9.7˚C – 12˚C) but our sample size precluded this analysis.

Comparison of embryonic otoliths, hatch day otoliths, and post-hatch otoliths of young cabezon enabled the identification of the first full increment as a distinct hatch mark. While embryonic increments were often faint and rarely formed a complete ring around the primordium, the hatch mark was the first dark increment, often followed by a bright, translucent zone, that could be traced at least three-quarters of the way around the primordium. This hatch mark occurred at ~18µm in all larvae up until 4dph. In individuals collected after 4dph, the average location of the hatch mark decreased (i.e., was closer to the primordia), suggesting that the individuals who survived longest were, on average, smaller at hatch. We also found that the individuals that survived the longest (14dph) were significantly smaller at 1-4dph compared to individuals collected at earlier ages. This suggests that a smaller size increases tolerance to starvation, perhaps because similar amounts of initial yolk sac can extend over a longer period for a smaller individual.

The significant relationship between fish size and otolith size in field-collected juvenile cabezon confirms that otolith-derived growth metrics reflect proportional changes in fish size (Thorrold and Hare, 2002). Because this relationship is consistent across a wide range of fish sizes and ages, and from fishes that experienced highly variable environmental conditions across five years, we conclude that otolith-derived growth measurements can be used to interpret cabezon biology and ecology. Additionally, we found the pelagic phase of juvenile cabezon to range from 2.1-4.3mo. A previous study in California found the pelagic phase of cabezon to last 3-4mo, based on the disappearance of larvae from the plankton and the arrival of juveniles into demersal intertidal habitats (O'Connell, 1953). The wider range that we found couple be attributed to 1) more precise estimation of the pelagic duration using otolith analysis, 2) latitudinal variation in pelagic duration, and/or 3) the ability to advance or delay metamorphosis and settlement, which has been found in other species to be an adaptation to maximize synchrony with advantageous environmental conditions (e.g., lunar phase; Sponaugle and Cowen, 1994, 1997; Rankin and Sponaugle 2014). There remains much to be learned about the growth, survival, recruitment, and population dynamics of cabezon from the examination of early life history traits across using juvenile otolith microstructure analysis (Wilson 2022). Identifying the mechanisms that translate environmental conditions into adult population dynamics through exploration of early life history traits is the focus of ongoing study in multiple fisheries research groups.

Our interpretation of the 'abnormal' otolith growth pattern in both reared larvae and wild-caught juvenile cabezon is that it indicates premature hatching. The early hatch mark in abnormal otoliths indicates that reared hatchlings were much smaller-at-age than individuals that followed a normal growth pattern. They also remained relatively small through 4dph. The wider otolith increment widths that followed this early hatch mark may reflect faster growth fueled by more yolk reserves relative to individuals with normal growth who would have consumed more yolk prior to hatching. As further support for this interpretation, we note that the fast growth apparent in abnormal otoliths declined precipitously after 4d, which aligns with absorption of the yolk sac. Overall, these patterns suggest that there is plasticity in hatch timing, hatch size, size-at-age, and growth rate in the earliest life stages of cabezon. Because cabezon are known to spawn in a variety of habitats (Feder et al., 1974; Lauth, 1987) and throughout the year (O'Connell, 1953; Lauth, 1987, 1989), eggs may encounter diverse environmental conditions and thus variation, even within a single brood, may be adaptive.

Acknowledgements

We are grateful to the Oregon Coast Aquarium, without their willingness to provide a cabezon brood this study would not have been possible. More than 60 individuals assisted with the collection and measurement of the juvenile fish samples. We especially acknowledge the efforts of Tully Rohrer, Jerod Sapp, James Burke, Joe Tyburczy, Tim Foley, Dani Ottmann, Will Fennie, Kelsey Swieca, Cameron Royer, Tom Calvanese, Amanda Olmos, Madeleine McArthur, Aliona Megedyuk, and the Oregon Department of Fish and Wildlife (ODFW) Marine Reserve Program team, including Brittany Huntington, Lindsay Aylesworth, Jessica Watson, Keith Matteson, Wolfe Wagman, Neal McIntosh, Ashley Knight, Cori Kane, Stephanie Fields, and Ryan Fields. Multiple funding sources supported this project including Hatfield Marine Science Center and Oregon Sea Grant awards to M.W. S.S. was supported during this study and its preparation for publication by National Science Foundation grant OCE 2125407; K.G.C. was supported by the Ocean Science Innovation Fund at Oregon State University. This study was supported in-kind by ODFW and the Oregon Coast Aquarium.

Contributions

M.W., S.S., and K.G.C. designed this study. M.W. conducted lab analyses, field collection, and data analysis. M.W., S.S., and K.G.C. prepared the manuscript.

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Figures

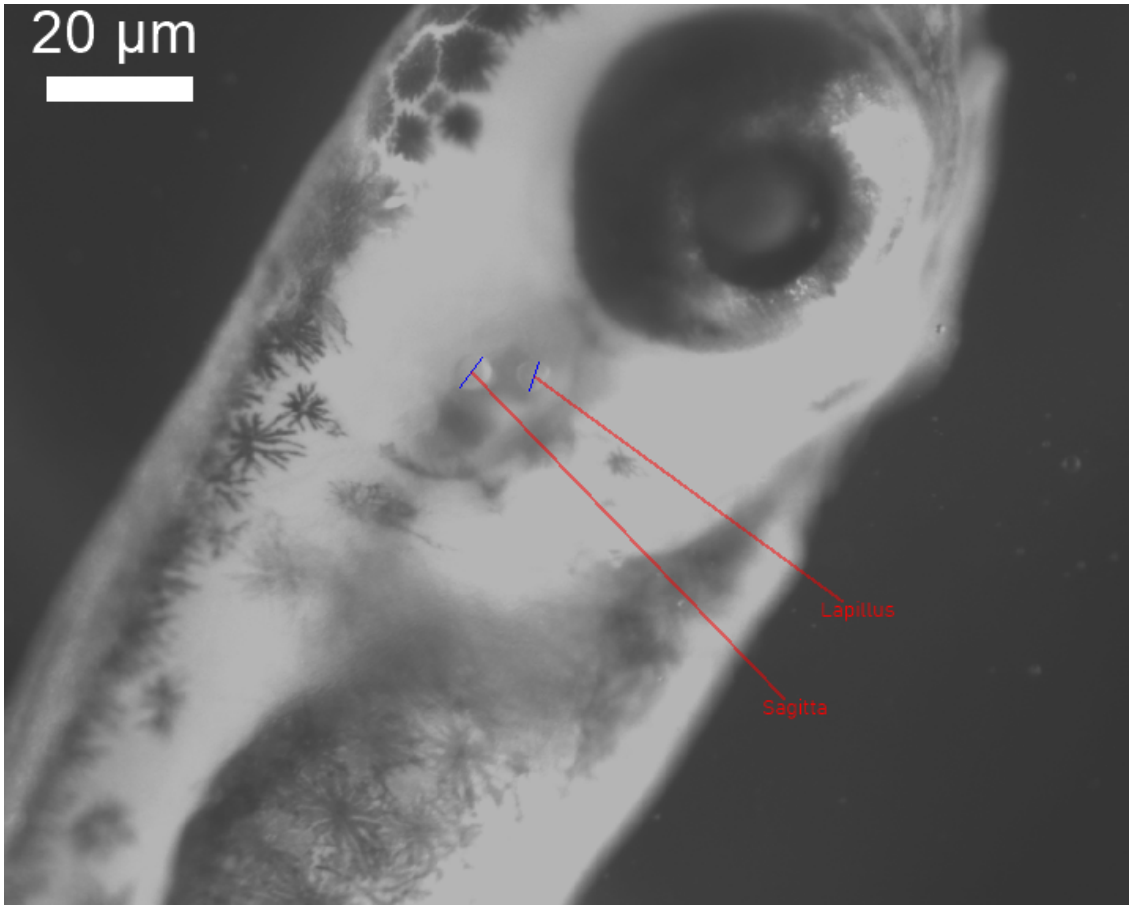


Figure 1. The cranium of a larval cabezon (*Scorpaenichthys marmoratus*). In older larvae, the sagitta is larger than the lapillus, but in younger larvae, the sagitta is identified by its medial position in the cranium.

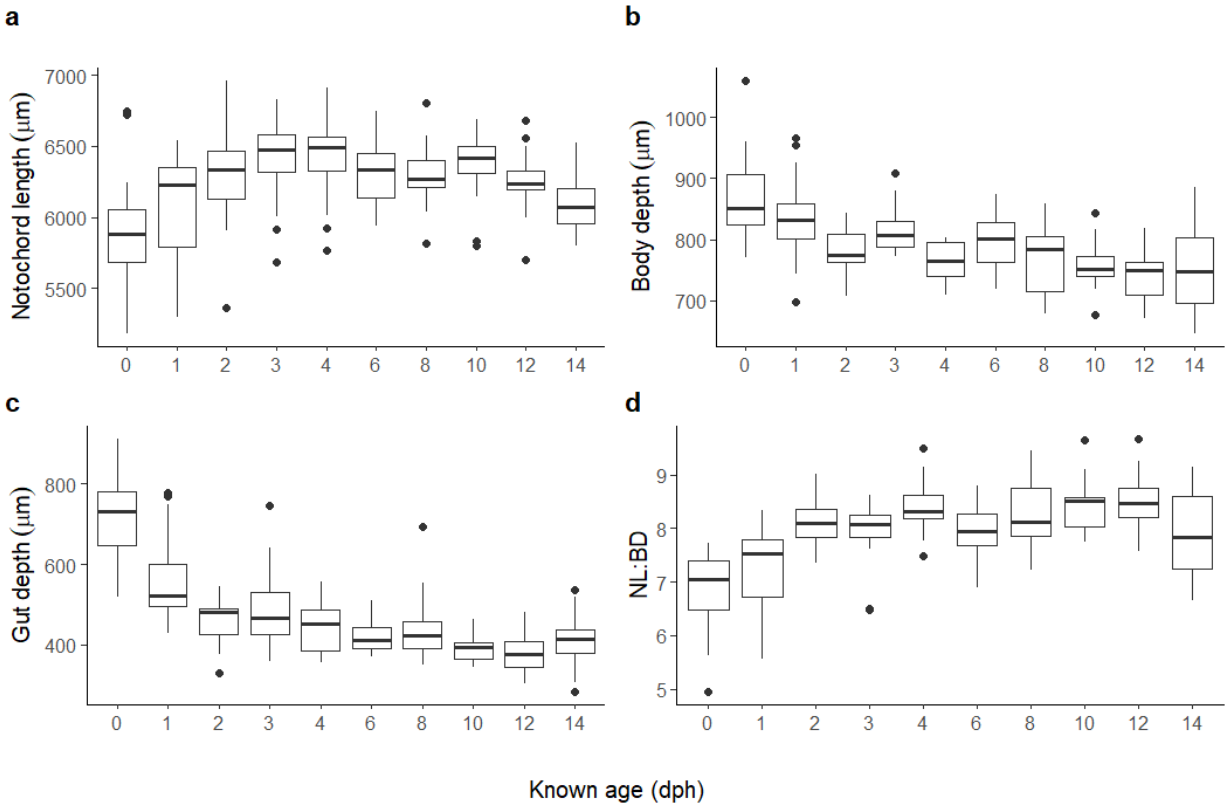


Figure 2. Morphometric measurements of cabezon notochord length (L_N), body depth, gut depth, and the ratio of L_N to body depth as a function of known age. All larvae were reared and subsampled (n=20 per dph) for 14d from captive bred eggs.

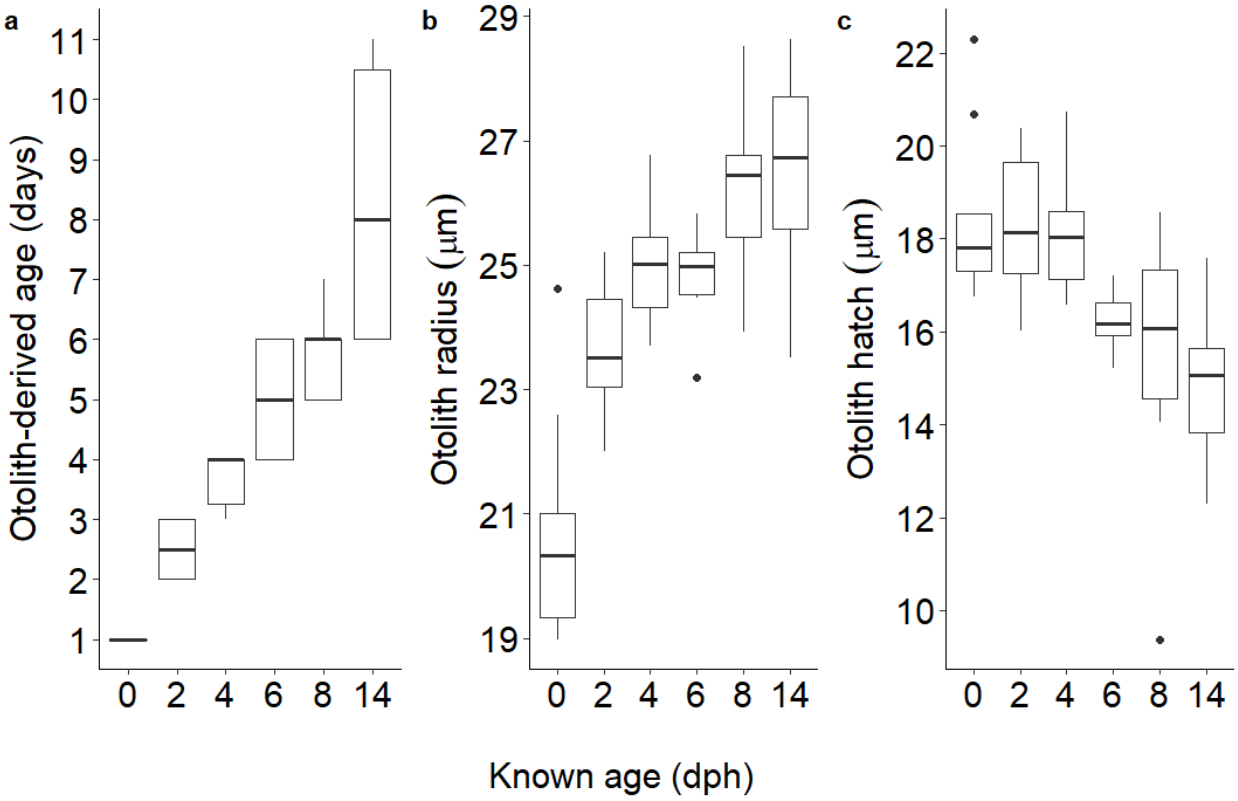


Figure 3. Otolith-derived age, otolith radius, and otolith hatch location for each stage in which otoliths were examined. Otolith-derived age matches known age until 4dph, after which they become decoupled. Otolith radius increases with known age, and otolith hatch radii decreases with age. All larvae were reared and subsampled (n=5 per dph) for 14d from captive bred eggs.

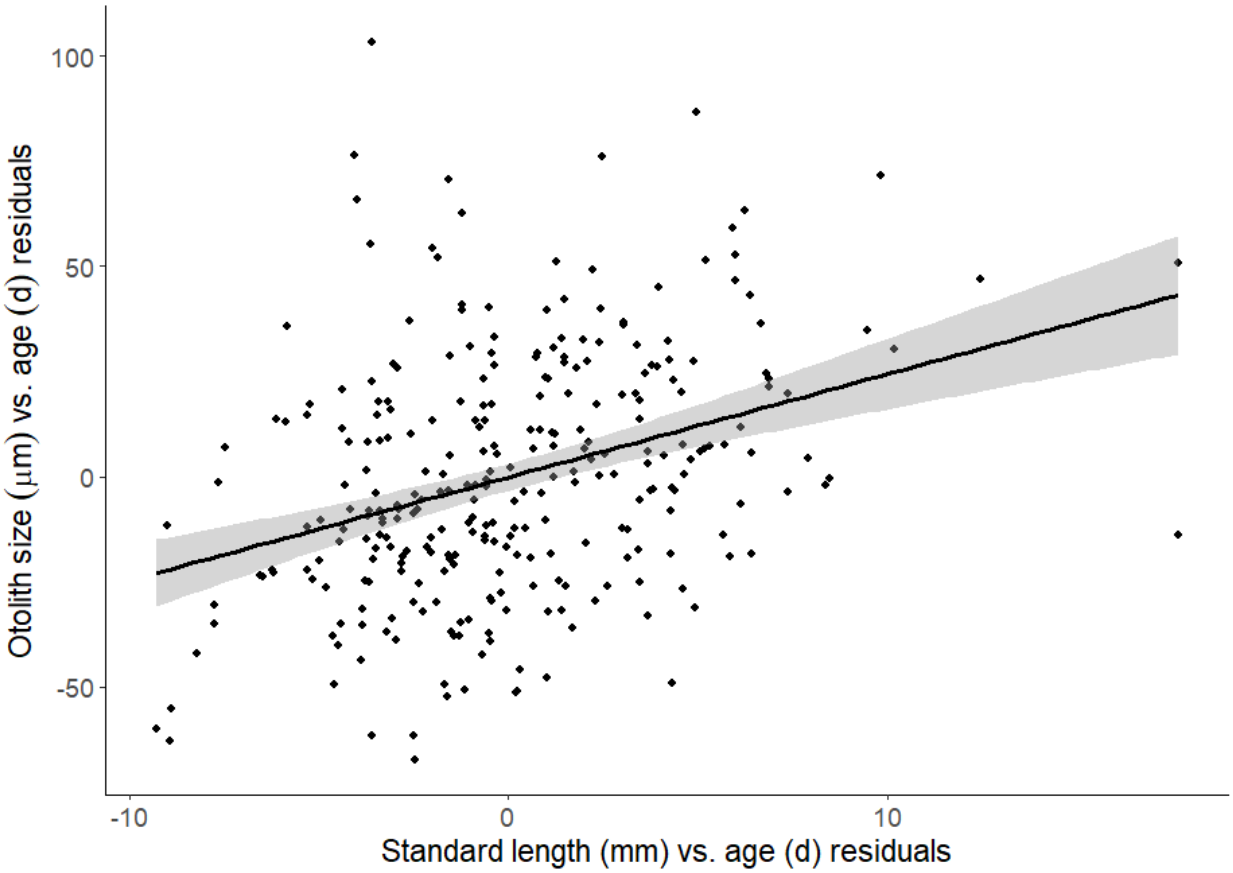


Figure 4. Field collected juvenile cabezon otolith size vs. age residuals regressed on fish standard length (L_s) vs. age residuals. Line equation is $Y = -0.15 + 2.45X$ ($R^2 = 0.12$; $P < 0.001$). Juveniles collected over five years from traps deployed nearshore off the coast of Oregon.

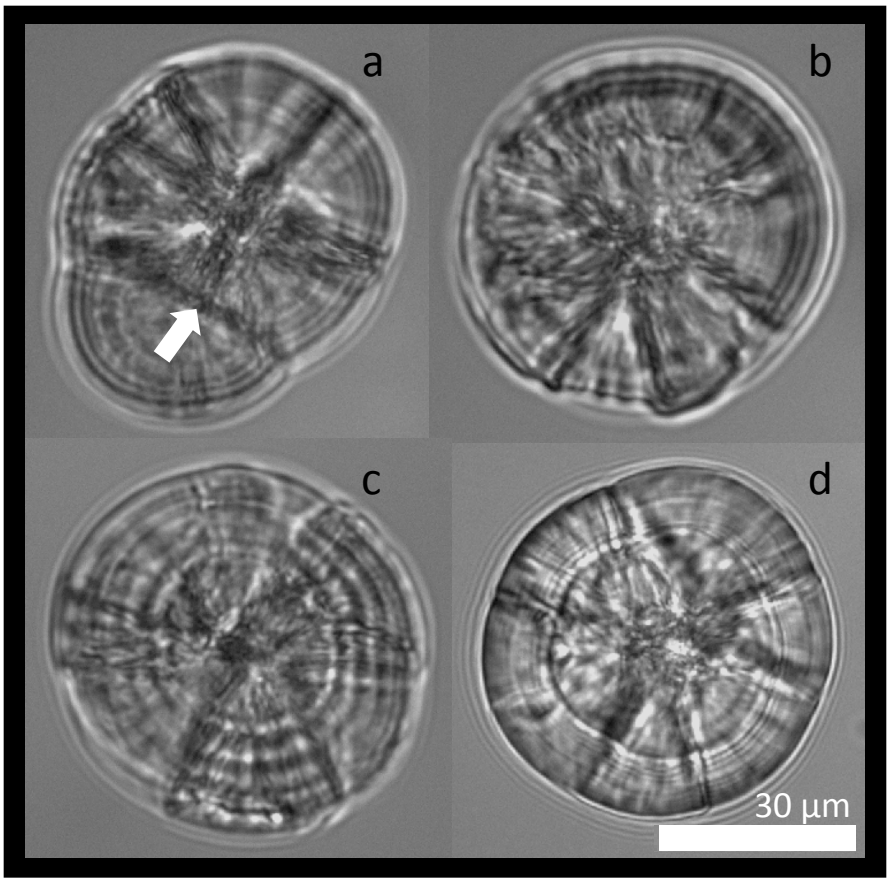


Figure 5. Abnormal otoliths of reared cabezon larvae. (a) and (b) illustrate asymmetry between left and right otoliths from a single individual at 8dph. (a) also illustrates an early secondary primordia (arrow). (c) and (d) are sagittal otoliths from two 14dph individuals. (c) illustrates an abnormal growth pattern, which could be indicative of premature hatching and/or compensatory fast growth due to stress. This is contrasted with the more commonly observed growth pattern in (d). Note that although the individual in panel (d) is 14dph, there are only 11 increments after the hatch mark, illustrating a decoupling of age and increment number.

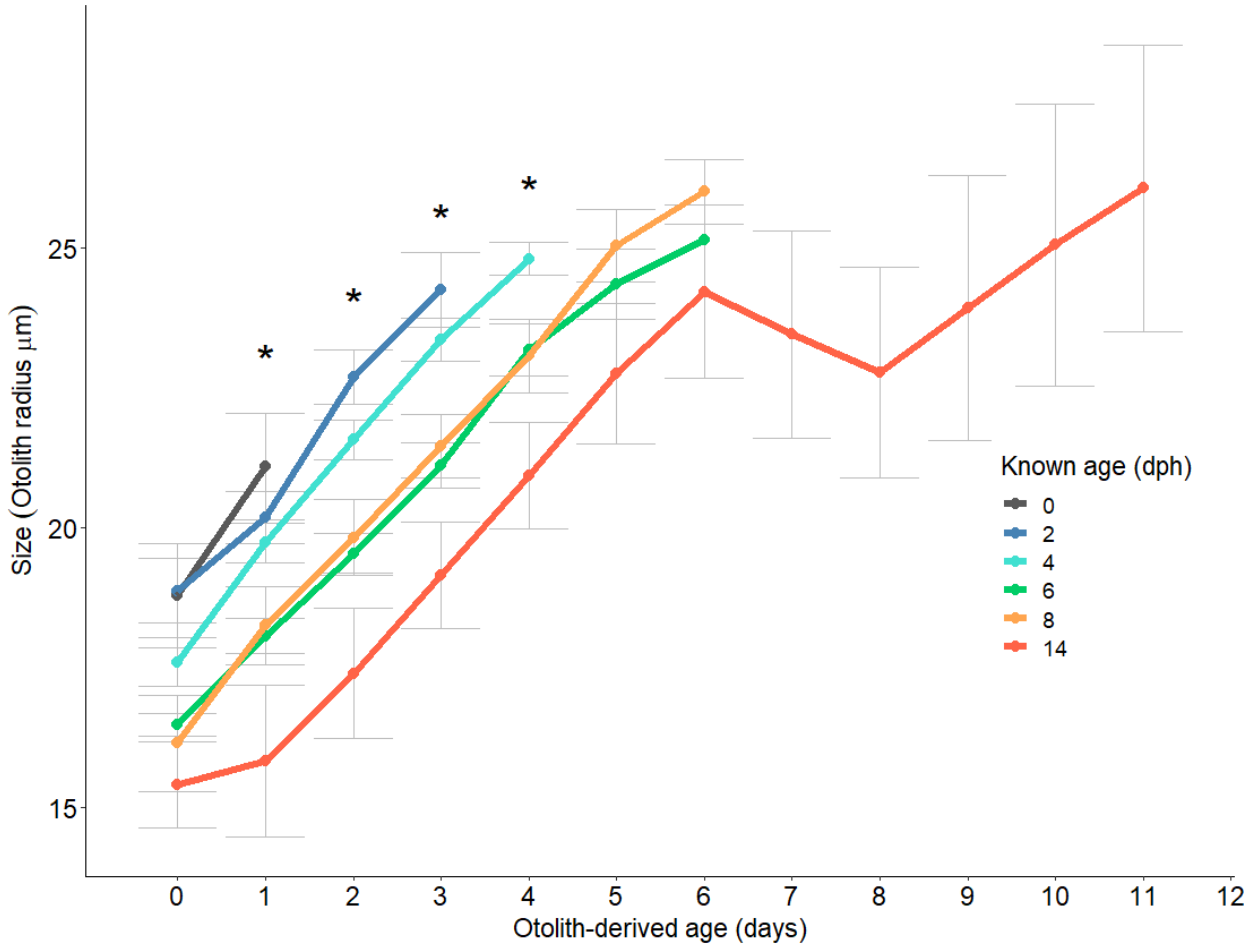
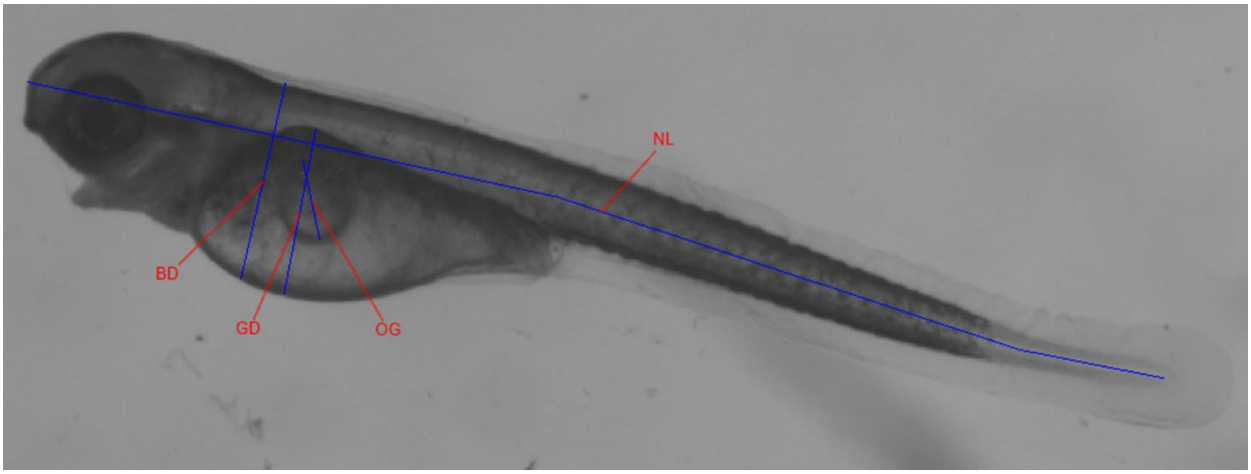
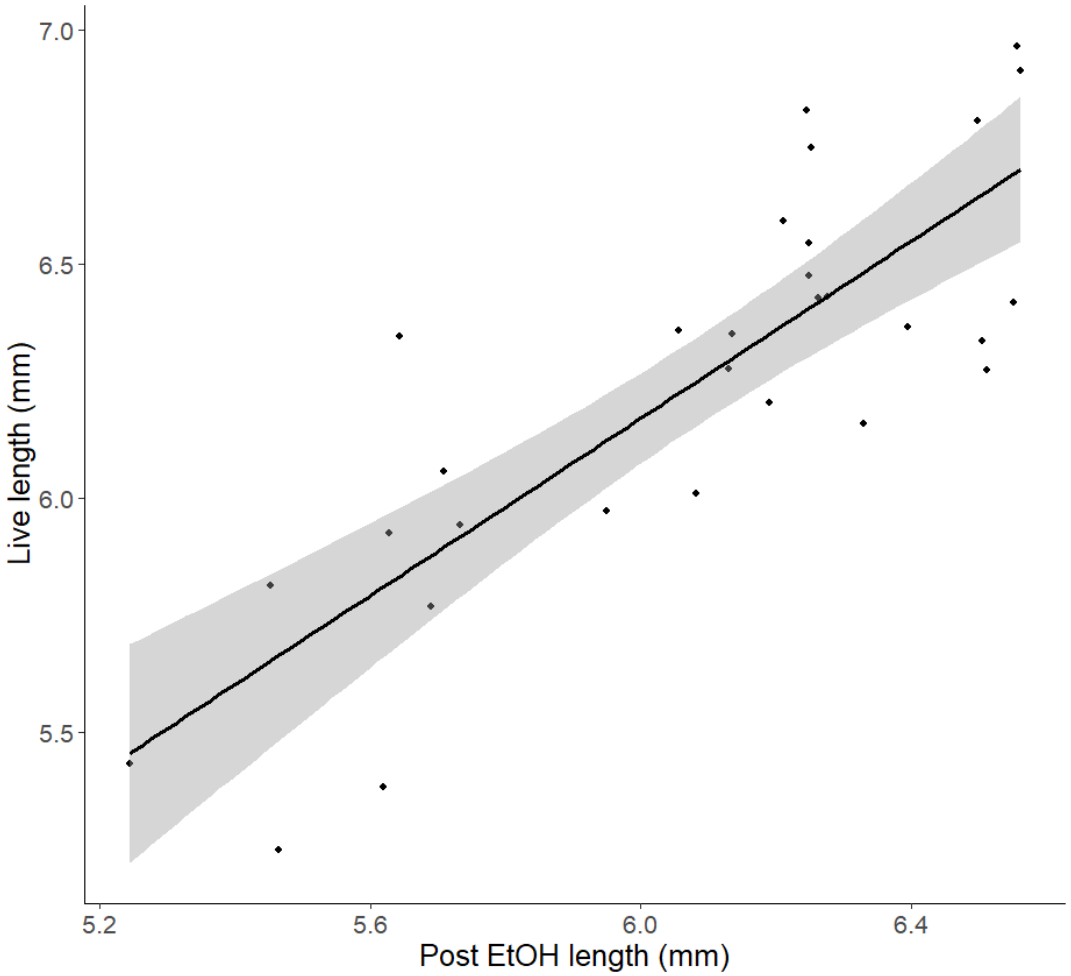


Figure 6. Mean size-at-age of reared cabezon larvae as a function of their otolith-derived age. Individuals that survived longer were smaller at a given age. 14dph individuals were significantly smaller than 0, 2, and 4dph individuals at ages 1-3 d. At age 4 d, 14 dph individuals were significantly smaller than 4dph individuals. Error bars represent the standard error of the mean.

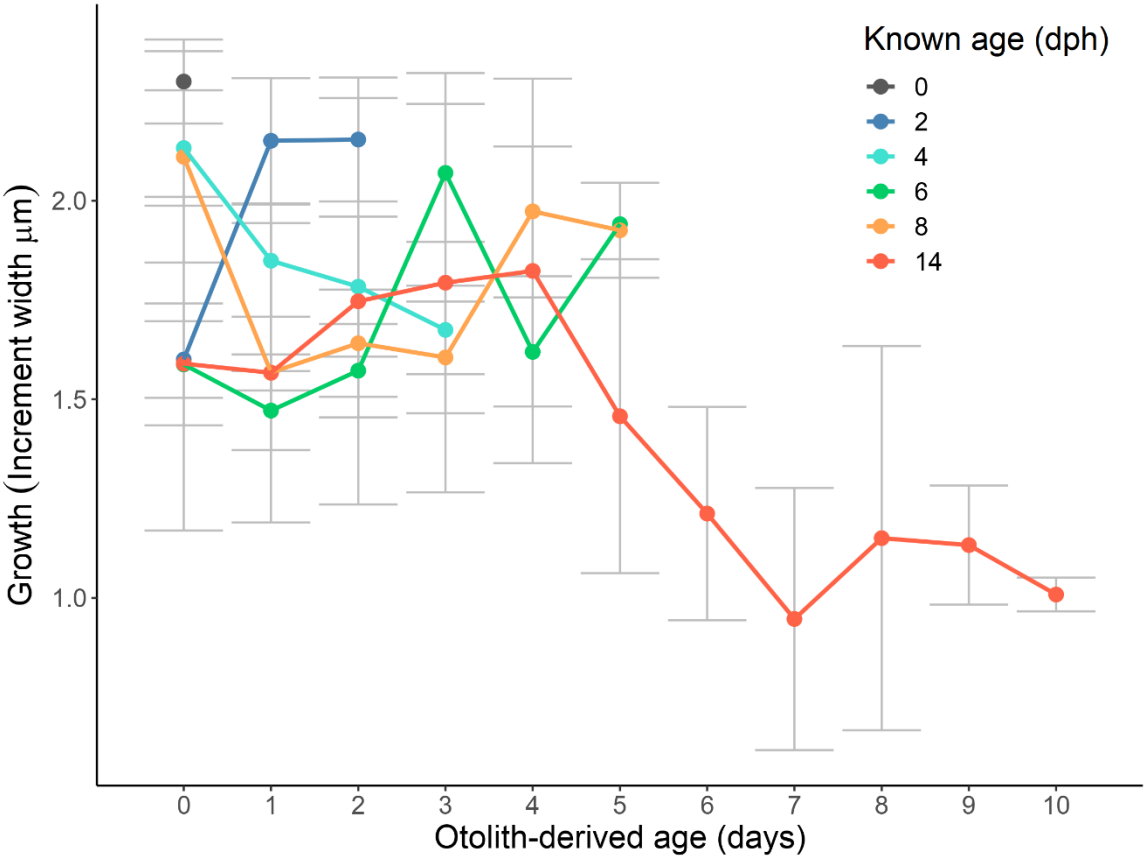
Supplemental Figures



S1. Morphometric measurements of reared cabezon larvae included notochord length (L_N), body depth (BD), gut depth (GD), and size of the oil globule (OG). In older larvae, there was no clearly visible oil globule.



S2. Notochord length (L_N) of live cabezon larvae regressed on post-preservation (EtOH) L_N to yield the shrinkage factor in preserved larvae. Line equation is *Y=0.49 + 0.95X* (R^2 = 0.67; P<0.001).



S3. Mean growth (measured by increment width in microns) as a function of otolith-derived age (days). Individuals that survived the longest had a precipitous decline in growth after 4dph, likely corresponding to yolk sac absorption, though these differences are not significant due to small sample sizes (n=5 per dph).