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Short communication

Age and growth of recently settled splitnose and redbanded rockfishes in the northern California Current



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ABSTRACT

Growth is key to the survival of fishes during their early life and ultimately affects annual recruitment to adult populations. To evaluate early life history traits of two commercially harvested fishes, splitnose ($Sebastes \ diploproa$) and redbanded ($S.\ babcocki$) rockfishes, we examined the otolith microstructure of juveniles of both species that settled simultaneously in an unusually large settlement pulse. Although overall growth during the dispersal phase was similar for both species, splitnose rockfish were ~ 2 wks younger and smaller in length at time of sampling, encompassed a narrower age range, and had higher prevalence and earlier occurrence of accessory primordia in their otoliths. Despite almost identical morphological traits of juveniles, our results suggest different pelagic strategies. The otoliths of splitnose rockfish grew faster during a 30-d period, reflecting either faster somatic growth during this period or a different rate of otolith deposition.

1. Introduction

Fishery management of marine fishes with complex life histories is most effective when applying a holistic approach that includes fishery-, oceanographic-, and early-stage ecological data (Hare, 2014). During the pelagic larval and juvenile phases, environmental conditions influence the early life history traits and survival of fishes that subsequently enter the adult population (Houde, 2008; Landaeta et al., 2015). Thus, quantifying early life history traits is critical to evaluate spatially and temporally variable mortality, improve dispersal models (Cowen et al., 2000), and ultimately, attain a better understanding of the factors influencing population replenishment. Unfortunately, our knowledge of these early life traits is limited for a number of fish taxa, including the diverse and fishery-important rockfish species in the Sebastes genus. Rockfishes are long-lived (up to 100 yrs) and late-maturing species that generally range from Alaska, United States, to Baja California, Mexico. Rockfish eggs hatch inside the mother's uterus, and larvae are released (parturiated) to disperse in the pelagic environment for several months before settling and recruiting to the benthic fish community (Love, 2011). Otolith-derived traits such as pelagic duration, daily growth, and size-at-age of individual fish can reveal different life history strategies that fishes employ to survive the pelagic phase and, for benthic species, reach their settlement habitat (Rodríguez-Díaz and Gómez-Gesteira, 2017). Further, coupling individual-based otolith data with oceanographic information allows evaluation of the different environmental conditions that affect growth, survival, and pelagic larval duration (PLD) (Shulzitski et al., 2016).

Here we used otolith microstructural analysis to evaluate patterns of growth, daily size-at-age, and settlement size and age of recently settled juvenile splitnose (*S. diploproa*) and redbanded (*S. babcocki*) rockfish. Both species inhabit relatively deep (mostly 150–450 m) habitats of the California Current System (CCS) and are thought to have a particularly long pelagic duration that can extend up to one year (Love, 2011). As newly settled juveniles, these species are morphologically similar and often appear together, which can confuse their identification and suggests hypothetically similar pelagic life histories (Love, 2011; Ottmann et al., 2017, 2018). Although these species are prominent members of the temperate rockfish guild—and they are commercially harvested by trawling, longline, and hook-and-line fisheries from British Columbia to Central California (Love, 2011)—relatively little is known about the early life history of either species.

2. Materials and methods

Newly settled juvenile fishes were collected from the Oregon coast using Standard Monitoring Units for the Recruitment of Fishes (SMURFs; Ammann, 2004). Seven replicate SMURFs were deployed for 15 d (August 27–September 11, 2013) at 1 m below the surface as part

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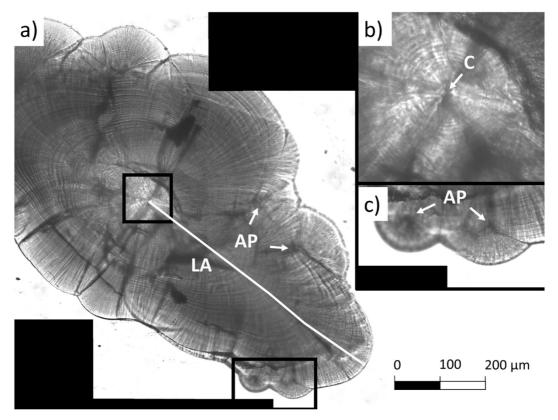


Fig. 1. Left sagittal otolith of a splitnose rockfish (Sebastes diploproa). Areas framed by black boxes are zoomed in for better resolution of the (a) core and (b) accessory primordia. LA = longest axis; AP = accessory primordia; C = core.

of a longer recruitment time series [see Ottmann et al., 2018 for a complete description of collectors, deployment, and sampling methodology]. Rockfish recruitment to coastal Oregon is episodic and typically relatively low; however, over this 15-d sampling period, a total of 538 splitnose and redbanded rockfishes were collected from the SMURFs, providing an unusual opportunity to compare the two *Sebastes* species. Fish were measured (standard length), and samples from 491 individuals were sent to the National Oceanic and Atmospheric Administration (NOAA) Southwest Fisheries Science Center in Santa Cruz (California) for genetic identification (Ottmann et al., 2017), revealing 88.2% splitnose rockfish and 11.8% redbanded rockfish.

Sagittal otoliths from 90 splitnose juveniles and 35 redbanded were dissected, cleaned, and imaged using standard procedures (Sponaugle, 2009). Otolith increments were assumed to be daily as deposition has been validated for splitnose rockfish (Boehlert, 1981) and other rockfish species (e.g. Laidig et al., 1991). Otolith increments were counted and measured along the longest axis from core to edge (Fig. 1a-b). We followed standard repeated count procedures after Shulzitski et al. (2016), and usable reads were obtained for a total of 32 splitnose and 28 redbanded rockfishes. In addition to daily increments, we enumerated the number and location of secondary (or accessory) primordia in the anterior portion of each otolith (Fig. 1c). These secondary growth centers are often associated with major changes in fish development during the early life stages (reviewed in Jones, 2009). We did not consistently observe any change in the increment pattern that could be considered a settlement mark, thus we assumed the sampled juveniles could have settled at any time within the 15-d sampling window.

To compare size, age, and growth between the two species we applied Welch's 2-sided *t*-tests to somatic length (SL), age (number of otolith growth increments) and overall growth rate (SL/age at settlement). To confirm that otolith growth could be used as a proxy for somatic growth, we regressed otolith length-at-age residuals against somatic length-at-age residuals (Thorrold and Hare, 2002). We also

examined mean daily otolith growth (mean increment width each day of life) and mean size-at-age (otolith radius-at-age) trajectories over the life of each species. We truncated the plots of the trajectories at later ages to maintain a minimum n=10 for each day and species. Welch's 2-sample t-tests were used to evaluate growth differences between both species at Days 25, 50, and 75, and to compare the age at which the first accessory primordia occurred. We tested assumptions of normality prior to significance tests and considered differences to be significant at <5% p-value. Length and age results are presented as mean \pm standard deviation and range. All analyses were conducted in R v3.3.2 (R Core Team, 2017) using package 'tidyverse' v1.1.1 (Wickham, 2017). Fish-standard length data and otolith data are available from the Open Science Framework repository: https://osf.io/kdjw2/.

3. Results

Recently settled splitnose rockfish (28.1 \pm 3.4 mm; 23.1–38.2 mm) were significantly (t₄₉, p=.002) smaller than redbanded rockfish settling during the same cohort window (31.6 \pm 4.7 mm; 22.9–40.9 mm; Fig. 2a-b). Similarly, the mean pelagic duration of splitnose rockfish (95.1 \pm 12.7 d; 77–127 d) was 13.5 d shorter (t_{50.7}, p<.001) than that of redbanded rockfish (108.6 \pm 16.3 d; 79–143 d). Based on size and age at settlement, overall mean growth during the pelagic phase of both species was similar (t_{44.4}, p=.689): splitnose rockfish = 0.293 \pm 0.004 mm $\,$ d $^{-1}$; redbanded rockfish = 0.297 \pm 0.025 mm d $^{-1}$.

Somatic and otolith length-at-age residuals were positively related for both species (F, p < .001; SM Fig. 1), indicating that otolith growth can be used as a proxy for somatic growth (Thorrold and Hare, 2002). Although overall growth rates were similar between the two species (above), daily otolith growth trajectories revealed notable differences between species (Fig. 2c). Growth followed a similar trajectory until Day 25 ($t_{55.5}$, p = .114) but peaked higher for splitnose around Day 50

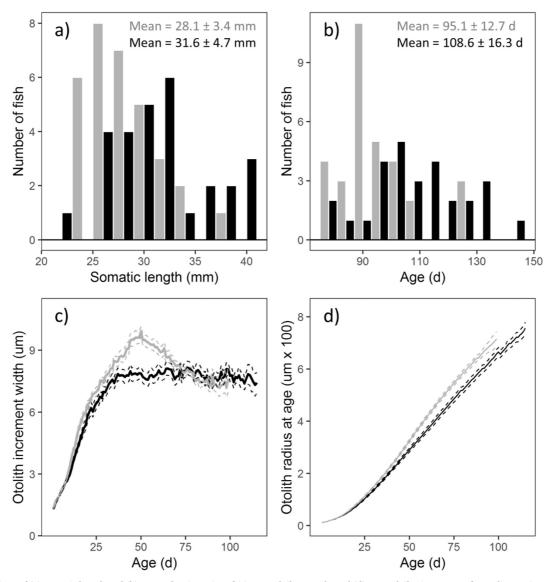


Fig. 2. Distributions of (a) somatic length and (b) age and trajectories of (c) mean daily growth, and (d) mean daily size-at-age of 32 splitnose (gray; S. diploproa) and 28 redbanded (black; S. babcocki) rockfishes. Solid lines indicate mean values; dotted lines indicate standard errors.

($t_{54.5}$, p < .001) and remained higher up to Day 75, when it leveled off to growth that was similar to redbanded rockfish ($t_{47.6}$, p = .894). These also resulted in different sizes at age—splitnose rockfish were significantly larger at age starting at Day 25 ($t_{56.3}$, p = .015; Fig. 2d).

For both species, accessory primordia occurred at up to three different areas (i.e. originating at specific growth increments) in the otolith, but accessory primordia were more prevalent in splitnose rockfish (n=31/32) than in redbanded rockfish (n=22/28). The first increment occurred on average 26.9 d earlier in splitnose rockfish than in redbanded rockfish ($t_{31.9},\ p<.001$). Occasionally, more than one primordia occurred at the same growth increment.

4. Discussion

Although several early life history traits such as morphological appearance and settlement timing are relatively similar between splitnose and redbanded rockfishes, otolith microstructural analysis of this large settlement cohort suggests that some ecological traits could differ. Splitnose juveniles were on average 3.5 mm smaller than redbanded juveniles, yet they settled almost two weeks earlier (younger age). This translated into a mean growth rate of $\sim\!0.3\,\mathrm{mm}$ d $^{-1}$, which was almost identical to the mean growth of redbanded rockfish. Even though all

fishes settled during roughly the same time, standard length and age ranges of splitnose rockfish were narrower than that of redbanded rockfish, indicating that the parturiation period was either less protracted than that of redbanded rockfish or that individuals that parturiated within this period experienced enhanced survival in the plankton compared to earlier or later cohorts. Either way, the fact that these splitnose settlers had a narrower age range at settlement suggests that survivors within this cohort experienced less overall environmental variability in the plankton across the dynamic environmental conditions in the CCS.

The overall pelagic growth rate (~0.3 mm d⁻¹) was similar between our two study species as well as compared to other juvenile rockfishes (see Laidig et al., 2008). Younger larval stage rockfishes often have slower growth rates (~0.1–0.2 mm d⁻¹; Landaeta and Castro, 2006, Laidig et al., 2008). The pelagic growth rate reported here is also comparable to the growth of pelagic larval stages of many other pelagic and demersal fishes (e.g. Jenkins and Davis, 1990; Allen and Block, 2012). Despite the resemblance in overall growth rate of splitnose and redbanded rockfish juveniles, analysis of the daily growth trajectories indicates important variation in growth over time. Splitnose rockfish exhibited significantly faster growth than redbanded rockfish for an approximately 30-d period between Days 35–65, reflecting either

faster somatic growth during this period or a different rate of otolith deposition. Given that redbanded rockfish spent \sim 2-weeks longer in the plankton, the faster growth of splitnose did not translate into larger size-at-settlement.

The two rockfishes also differed in the occurrence of accessory primordia. These primordia have previously been linked to ontogenetic changes such as metamorphosis of recently settled fish (Campana, 1984) or the transition of rockfish larvae to pelagic juveniles (Laidig, 2010; Wheeler et al., 2017). For both of our study species, we found no consistent settlement mark near the otolith edge, but accessory primordia were observed in up to three different locations prior to the day of collection. Given that both species tend to associate with drifting kelp during their pelagic juvenile stage (Love, 2011), we hypothesize that accessory primordia develop during such events, and then again when juveniles settle to the canopy of coastal vegetation. While testing this hypothesis is beyond the scope of the present study, if true, the earlier and more prevalent accessory primordia in splitnose rockfish would suggest an earlier association with drifting kelp.

Compared to redbanded rockfish, splitnose rockfish from this settlement cohort were parturiated later and over a narrower window of time. They may have grown faster for a 30-d period, but they settled two weeks younger at smaller sizes. According to the growth-mortality hypothesis, fast-growing fishes that spend less time in the plankton are predicted to experience higher survival (Anderson, 1988). Our observations are consistent with this hypothesis - we collected almost 7.5× as many splitnose as redbanded juveniles during the same sampling interval. Large settlement events of multiple species are relatively rare in the CCS. Comparing interspecific growth trajectories of fishes that settled simultaneously provides a level of standardization of environmental conditions experienced by the settlers, which is useful for comparing interspecific growth differences. However, we acknowledge the limitations of a single, large settlement cohort analysis. Differences in early life history traits both within and between species should be examined in relation to variation in the environment. It is possible that early life history traits of fishes recruiting in this unusually large settlement cohort were atypical. Should the data become available in the future, analysis of multiple cohorts of both species would help test this hypothesis.

Author contributions

K.G.-C. and S.S. designed the research; D.O. and K.G.-C. collected field samples; D.O. analyzed the samples and data; all authors discussed the results and wrote the paper.

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collected under NMFS permit #18058, and fish protocols were approved by OSU Animal Care and Use Protocol #4183.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.seares.2019.03.002.

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