

Age validation of four rockfishes (genera *Sebastes* and *Sebastolobus*) with bomb-produced radiocarbon

Craig Kastle^{ID A,B}, Thomas Helser^A, Todd TenBrink^A, Charles Hutchinson^A,
Betty Goetz^A, Chris Gburski^A and Irina Benson^A

^ANational Oceanic and Atmospheric Administration, National Marine Fisheries Service, Alaska
Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115, USA.

^BCorresponding author. Email: craig.kastelle@noaa.gov

Abstract. In rockfish (Family Scorpaenidae), age determination is difficult and the annual nature of otolith growth zones must be validated independently. We applied routine age determination to four species of Gulf of Alaska rockfish: two shallower-water species, namely harlequin rockfish (*Sebastes variegatus*) and redstripe rockfish (*Sebastes proriger*), and two deep-water species, namely shortspine thornyhead (*Sebastolobus alascanus*) and shortraker rockfish (*Sebastes borealis*). The estimated ages (counts of presumed annual growth zones in the otoliths) were then evaluated with bomb-produced radiocarbon (^{14}C) and Bayesian modelling with Markov chain Monte Carlo simulations. This study successfully demonstrated the level of accuracy in estimated ages of redstripe rockfish (a 35% probability of underageing, and ~5% probability of overageing) and harlequin rockfish (a 100% probability that they were underaged by ~3 or 4 years). Measured $\Delta^{14}\text{C}$ in shortspine thornyhead and shortraker rockfish otoliths was lower and increased later than expected. Hence, incorrect age determination could not be evaluated. This is likely caused by dissimilar environmental and biological availability of ^{14}C between these two species and the Pacific halibut (*Hippoglossus stenolepis*) reference chronology, or underageing of these two species.

Additional keywords: age accuracy, age determination, Bayesian modelling, Markov chain Monte Carlo simulations, otolith, Scorpaenidae.

Received 7 September 2019, accepted 3 December 2019, published online 13 February 2020

Introduction

Rockfish (Scorpaenidae) are a valuable component of Alaska groundfish fisheries. The ex-vessel value of rockfish harvested in 2017 was ~US\$29 million (Fissel *et al.* 2019). The biological reference points used to determine harvest specifications for optimal management of a fishery stock depend on accurate fish age estimation (Parker *et al.* 2000; Tribuzio *et al.* 2017). A classic example of underageing is demonstrated with Pacific ocean perch (*Sebastes alutus*) when it was determined that interpretations of growth zones viewed on otolith's surface underestimated the ages relative to their cross-sections (Beamish 1979). In this example of Pacific ocean perch, the otolith cross-section ages provided a reduced estimate of natural mortality compared with that from otolith surfaces (Beamish and McFarlane 1983).

Fish age estimation relies on consistent methods of otolith preparation and interpretation of the otolith's annual growth zones. Two common methods of otolith preparation are the break and burn (Goetz *et al.* 2012a) and thin sectioning (Hutchinson *et al.* 2007). The interpretation of growth zones requires the application of a set of rules, or age determination criteria, in a consistent manner (Matia and Kimura 2012). This is

often difficult, and age estimates in long-lived species of fish suffer from low accuracy and precision (Campana 2001; Pearson and Gunderson 2003; Kimura and Anderl 2005; Hutchinson *et al.* 2007). Ideally, age determination criteria should be based on otoliths from fish of known age. However, such samples are rarely available, so validation of age determination methods by independent methods is required (Campana 2001; Kimura *et al.* 2006). Typically, ages are estimated by counting posited annual growth zones, and then a variety of age validation methods can be used to confirm that the estimated ages are accurate (Campana 2001; Kimura *et al.* 2006). If the estimated ages are deemed inaccurate by the validation method, the age determination criteria can be revised to correct a bias from the true age (Kastelle *et al.* 2017).

This study focuses on age determination in harlequin rockfish (*Sebastes variegatus*), redstripe rockfish (*Sebastes proriger*), shortspine thornyhead (*Sebastolobus alascanus*) and shortraker rockfish (*Sebastes borealis*). These species are managed by the North Pacific Fishery Management Council, with limited information on life history traits such as life span, proportion mature at age, size at age, mortality rates and population age structure. Because vital rates and life history

parameters for assessment models depend on reliable age data, it is necessary to validate age determination criteria and quantify age determination precision and bias, if it exists.

Previous research on age determination and age validation in redstripe rockfish, harlequin rockfish, shortraker rockfish and shortspine thornyhead is limited. For redstripe and harlequin rockfish, two species that occupy shallower water (Love *et al.* 2002; Rooper 2008) than most congener species, age validation information is not available. Otoliths in these two species exhibit growth patterns that are similar to northern rockfish, a species that is routinely aged for stock assessment with criteria validated using bomb-produced radiocarbon (Kestelle *et al.* 2016). Shortraker rockfish and shortspine thornyhead are found in deeper waters of the Gulf of Alaska (Love *et al.* 2002; Rooper 2008). Shortraker rockfish age determination has been attempted with resolved methods common to other Scorpaenids, but interpretation of growth zones is problematic with low precision between age readers (Hutchinson *et al.* 2007). Shortraker rockfish are thought to have a lifespan as high as 150 years (Munk 2001), which can exacerbate age reading difficulty. Radiometric age validation, using the ratio of $^{210}\text{Pb}/^{226}\text{Ra}$ in otoliths, confirms that they are long lived (Kestelle *et al.* 2000; Hutchinson *et al.* 2007). Unfortunately, confidence intervals (CIs) of radiometric age estimates become large in fish over ~60 years of age, and it does not provide information on individual fish. Age determination of shortspine thornyhead, also using common resolved methods, is similarly difficult with a maximum observed age of ~100 years. These methods and criteria have also been validated with the radiometric method (Butler *et al.* 1995; Kline 1996; Kestelle *et al.* 2000). In both these species, the interpretation of otolith growth zones is known to be problematic because of their compact and faint nature (Kline 1996; Hutchinson *et al.* 2007). The point here is, for all four species, resolved and established age determination methods and criteria exist, but need to be validated. This is based on the foundation of previous age reading in other Scorpaenids and the confirming age validation research.

In this study, we apply what is often considered the ‘gold standard’ method of age validation, bomb-produced radiocarbon (^{14}C) (Kalish 1995; Campana 2001; Kimura *et al.* 2006). This method relies on aboveground testing of atomic bombs conducted during the Cold War era, which caused a large increase in ^{14}C in the marine environment from the late 1950s to c. 1970 (Nydal 1993; Kumamoto *et al.* 2013). This increase is recorded in marine carbonates, including fish otoliths, formed during that era, providing a time reference. The amount of ^{14}C (measured as $\Delta^{14}\text{C}$) in otolith material deposited during the first year of a fish’s life (the birth year, calculated from the catch date minus the estimated age of the fish) can be compared to an established reference $\Delta^{14}\text{C}$ chronology (Piner and Wischniowski 2004; Wischniowski *et al.* 2015). So, in a simple evaluation, if $\Delta^{14}\text{C}$ values of test specimens (test specimens are those whose ages are under investigation) are synchronous with the reference chronology, then the ages estimated from counting growth zones is deemed accurate. In a more complex evaluation, the synchrony, or lack thereof, can be used to estimate the probability of ageing error (Kestelle *et al.* 2016). This age validation method has been successfully applied to several North Pacific species (e.g. Piner and Wischniowski 2004; Kerr

et al. 2005; Kestelle *et al.* 2008, 2016; Andrews *et al.* 2011; Wischniowski *et al.* 2015).

Age determination of redstripe rockfish, harlequin rockfish, shortraker rockfish and shortspine thornyhead is difficult. The methods and criteria used here for age determination are largely based on those used in other *Sebastes* species, and on variations of these methods. To facilitate the use of this age data in stock assessments, there is a need for new and better age validation. Therefore, our first goal was to use bomb-produced ^{14}C to validate ages estimated by otolith growth zone counts in all four species. Our second goal was to evaluate the probability of ageing error when these age determination methods and criteria are applied to these four species.

Materials and methods

Specimen collection

Shortspine thornyhead, shortraker rockfish, redstripe rockfish and harlequin rockfish otoliths were collected in the Gulf of Alaska from 1977 to 2015 during authorised National Marine Fisheries Service’s (NMFS) Alaska Fisheries Science Center (AFSC) scientific bottom trawl surveys and by NMFS fishery observers aboard commercial vessels (Fig. 1). Specimens selection was as explained for each species below, and was based, in part, on estimated birth years (using the age determination methods described in the following sections) such that the specimens were hatched during the era of increasing ^{14}C (see Tables S1–S4, available as Supplementary material to this paper).

Age determination and specimen selection

Redstripe and harlequin rockfish

Ages of redstripe and harlequin rockfish were estimated using the break-and-burn method (Goetz *et al.* 2012a) as part of routine age determinations by the AFSC Age and Growth Program to support fishery stock assessments. Interpreting the otolith’s innermost and outermost growth zones was typically the most difficult component of the age determination for these species. The innermost growth zones are difficult to interpret due to break-and-burn irregularities and the occurrence of indistinct or possibly non-annual growth zones. The outermost growth zones are difficult to interpret due to the compact nature of growth zones deposited in older adults.

Otolith selection for age validation was based on an initial sample of 446 redstripe rockfish and 563 harlequin rockfish that had been aged twice as part of routine quality control precision testing (Kimura and Anderl 2005). One of these age readings was done by an ‘expert age reader’ who had the most experience in applying the break-and-burn method and standard age determination criteria; the other was done by a second experienced reader (Fig. 2). Of this initial sample, we selected all specimens with estimated birth years (birth year = collection year – the expert age reader’s age estimate) before 1980 (redstripe rockfish; $n = 215$) and before 1983 (harlequin rockfish; $n = 108$) to ensure the era of marine radiocarbon increase would be represented. Next, when more than two specimens had the same estimated birth year, only two were randomly chosen for analysis. This process yielded 41 redstripe rockfish and 40 harlequin rockfish for bomb radiocarbon analysis (Tables S1, S2). For these chosen specimens, ages were independently

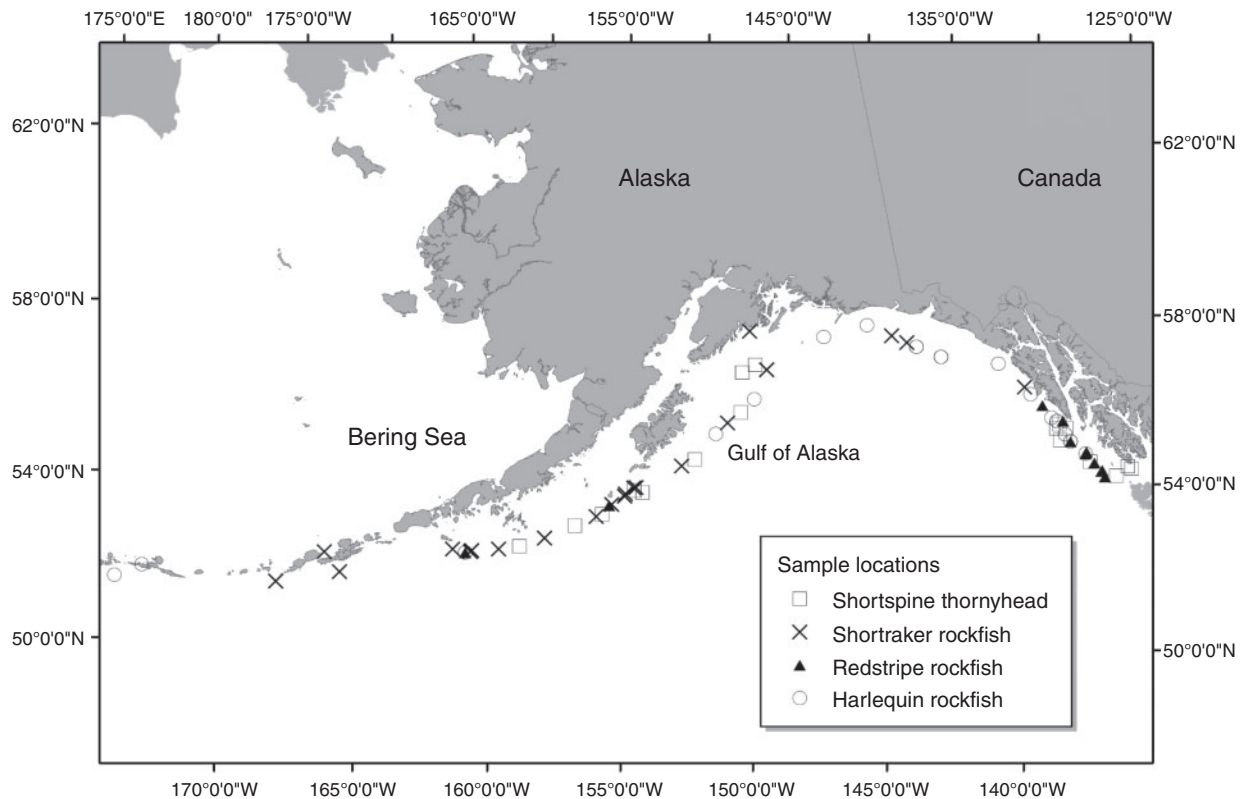


Fig. 1. Map of Gulf of Alaska collection locations for harlequin rockfish (*Sebastes variegatus*), redstripe rockfish (*Sebastes proriger*), shortspine thornyhead (*Sebastolobus alascanus*) and shortraker rockfish (*Sebastes borealis*).

estimated again by up to four different readers to provide up to six age estimates per specimen. The expert age reader's estimates of age were used as the validation ages to be tested.

Shortspine thornyhead

Shortspine thornyhead otoliths have historically been collected during AFSC scientific bottom trawl surveys, but they do not currently undergo routine age determination; therefore, previously aged specimens were not available. Otoliths from fish collected from 1996 to 2007 with lengths ≥ 24 cm were selected for age reading ($n = 66$). Longer specimens were used at the onset because we only needed older specimens that had birth years posited to be during the era of increasing bomb-produced ^{14}C .

Shortspine thornyhead otoliths were prepared and read using the thin-section method, similar to that established in Butler *et al.* (1995), Kline (1996), McCurdy *et al.* (2002), Hutchinson *et al.* (2007) and Goetz *et al.* (2012b). Otoliths were embedded in clear polyester resin and cut transversely through the core to produce thin sections (0.3–0.4 mm) that were then mounted on glass slides. Thin sections were coated with mineral oil and viewed under a dissecting microscope with reflected light and a black background (Fig. 2). The interpretation of growth zones and application of age reading criteria were difficult, especially for seemingly older specimens. There were often faint growth zones among those posited to form annually, as well as growth zones that did not conform to consistently spaced laminar patterns. A set of juvenile

shortspine thornyhead otoliths was surfaced aged and then broken transversely through the nucleus to help determine measurements of the first 3 years for each specimen.

Two different age readers (an expert and a second experienced reader) independently estimated the ages, and the average age was used to estimate the birth year for ^{14}C analysis. The average age was used because the shortspine thornyhead stock assessments do not use age-structured population dynamics models, are managed in a species complex (Echave and Hulson 2018) and because of the difficulty in interpreting otolith growth zones, even though they were aged by established methods and criteria. Hence, the average age was used here as the best way to make a starting point for age validation. Shortspine thornyhead specimens with posited birth years before 1979 were separated into two categories, those with ages ≥ 30 and ≤ 29 years (Table S3). In total, 9 specimens were randomly chosen from the older category and 20 specimens were randomly chosen from the younger category such that there were 3 or fewer specimens within any given birth year. The two categories were used to help incorporate as wide an age range as possible.

Shortraker rockfish

The shortraker rockfish selection process had minor deviations from that of the other three species. Shortraker rockfish otoliths were prepared for age determination by the same established otolith thin-section preparation methods and growth zone interpretations described for shortspine thornyhead

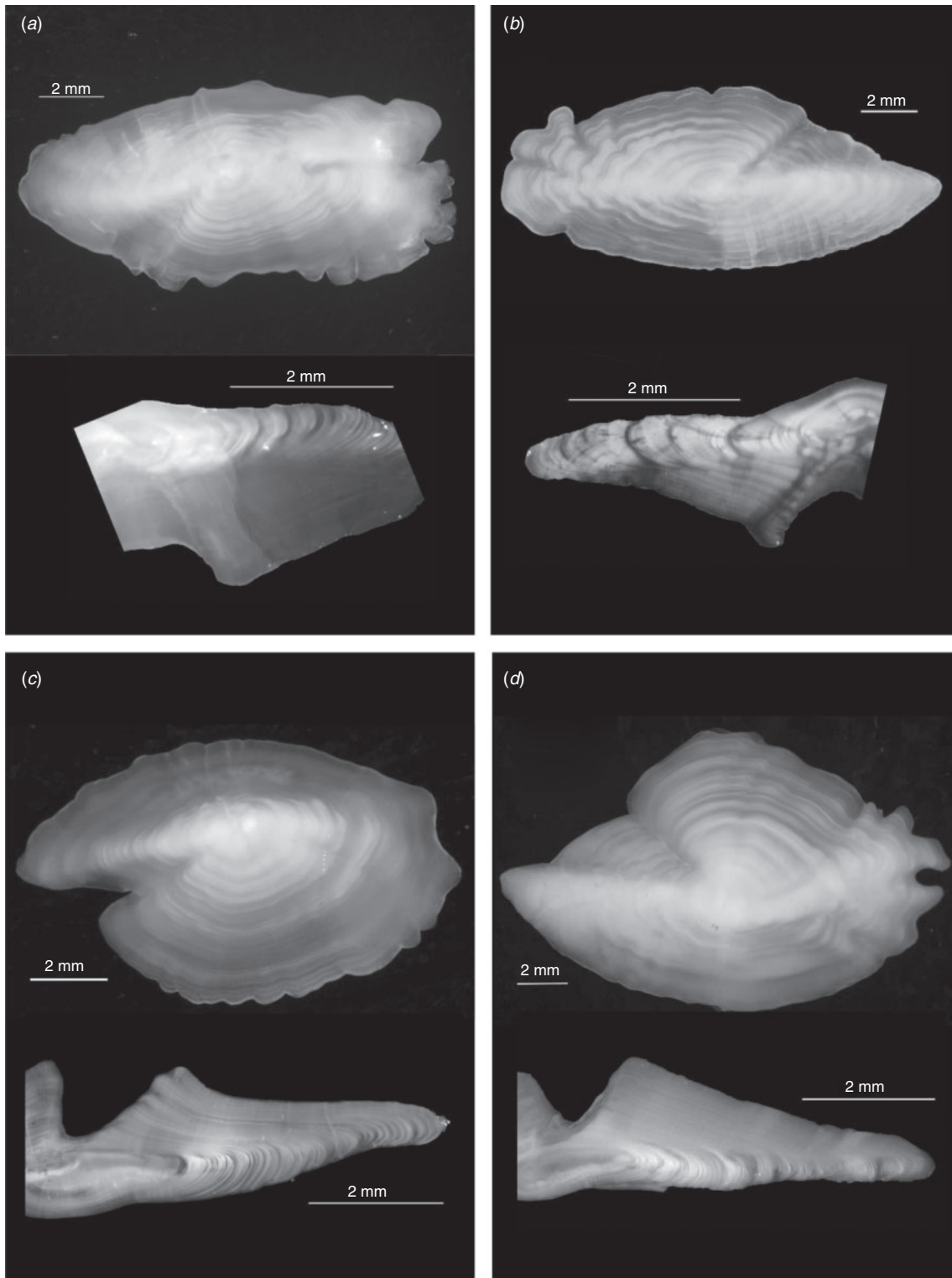


Fig. 2. Images of whole otoliths and break-and-burned preparations for (a) harlequin rockfish (*Sebastes variegatus*) and (b) redstripe rockfish (*Sebastes proriger*). Images of whole otoliths and thin-section preparations for (c) shortspine thornyhead (*Sebastolobus alascanus*) and (d) shorttraker rockfish (*Sebastes borealis*).

(McCurdy *et al.* 2002; Hutchinson *et al.* 2007; Goetz *et al.* 2012b; Fig. 2). Much like shortspine thornyhead, applying age reading criteria is difficult. To generate an adequate number of candidates, specimens collected between 1996 and 2006, and aged independently by two age readers (an expert and a second experienced reader; $n = 699$), were available. From those, specimens with estimated average birth years between 1952 and 1985 were considered. Similar to shortspine thornyhead, the average age of shortraker rockfish was considered the best way to make a starting point for age validation. Eighteen of the specimens were chosen because they were subjectively clear and the two age estimates differed by ≤ 5 years. Nine more specimens were chosen because there was a large difference between age estimates (7–20 years) and, subjectively, these otoliths were not clear and were difficult to interpret (Table S4). There was no regard for the number of specimens with the same estimated birth year.

Inter-reader precision and bias

All multiple readings per specimen were used to calculate 95% CIs for estimated ages and birth years. In the cases of harlequin and redstripe rockfish, up to six readings were used. In the cases of shortspine thornyhead and shortraker rockfish, just two readings were made and hence used to calculate the CIs. Only paired inter-reader readings (expert and second experienced reader) were used for precision statistics. Precision was evaluated by percentage agreement, average percentage error (APE; Beamish and Fournier 1981) and the CV (Chang 1982). Inter-reader bias (relative bias) was evaluated graphically using age bias plots (Campana *et al.* 1995). From the six readings of harlequin and redstripe rockfish otoliths, only the initial two age estimates (those of the expert and a second reader) were used to calculate precision statistics and construct age bias plots. In the instances of shortspine thornyhead and shortraker rockfish, just one set of paired readings was made.

Sample preparation and mass spectrometry

Age reading is a destructive process, therefore only one remaining otolith from each fish was available for ^{14}C examination. Cores from these otoliths, representing the first 2 years of life, were extracted to provide material for ^{14}C analysis. A 2-year core was necessary to meet the sample mass requirements of mass spectrometry. As a guide, target core sizes were determined on a per species basis by measuring the size and mass of otoliths from 2- and 3-year-old juvenile specimens. To extract each core, growth zones outside the first two translucent zones were removed (wet sanded) with a Buehler MetaServ 250 grinder-polisher (Lake Bluff, IL, USA^A). The inner two or three translucent growth zones typically became more visible as outer material was removed, and also served as a guide in this coring process. For more information on coring methods, see Kestelle *et al.* (2016) or Kestelle *et al.* (2008). The cores were cleaned ultrasonically in distilled and deionised water, dried, weighed, placed in acid-washed glass vials and shipped to the National Ocean Sciences Accelerator Mass Spectrometry Facility (NOSAMS) at the Woods Hole

Oceanographic Institution (WHOI; Woods Hole, MA, USA), where they were analysed for ^{14}C and ^{13}C . The results are reported as $\Delta^{14}\text{C}$ in per mille (Stuiver and Polach 1977) which represents the relative difference between ^{14}C activity in an international standard and the sample. Values of otolith $\Delta^{14}\text{C}$ were normalised to 1950, corrected for isotopic fractionation with $\delta^{13}\text{C}$ and normalised to a $\delta^{13}\text{C}_{\text{VPDB}}$ value of -25‰ (Woods Hole Oceanographic Institution National Ocean Sciences Accelerator Mass Spectrometry Facility 2018).

Age validation

To perform the age validation, the increase (pulse function) of the $\Delta^{14}\text{C}$ in the test validation rockfish otolith cores, as a function of birth year, was compared to a Gulf of Alaska Pacific halibut (*Hippoglossus stenolepis*) reference $\Delta^{14}\text{C}$ chronology (Piner and Wischniowski 2004). The Pacific halibut $\Delta^{14}\text{C}$ reference chronology is based on juvenile fish whose age is considered known, or without any error. We used a coupled-function model (product of Gaussian and exponential models; Hamel *et al.* 2008; Kestelle *et al.* 2016) as follows:

$$\hat{y}_x = \lambda + ke^{\left[\left(\mu \cdot r \right) + \frac{(\sigma^2 \cdot r^2)}{2} \right]} \times e^{(-r \cdot x)} \Phi(\mu + \sigma^2 \cdot r, \sigma, x) + \sigma_e^2$$

where \hat{y}_x is estimated $\Delta^{14}\text{C}$, x is birth year and the model parameters are: λ , average pre-bomb $\Delta^{14}\text{C}$ value (lower predicted asymptote); k , the total predicted increase of $\Delta^{14}\text{C}$ to reach the upper asymptote; μ , mean or peak year of radiocarbon Gaussian pulse curve (which is the birth year corresponding to the midpoint (50%) of the $\Delta^{14}\text{C}$ increase); σ , standard deviation of the Gaussian pulse curve; r , exponential decay rate (per year) of the post-peak decline; and σ_e^2 , the error variance. The symbol Φ represents the cumulative normal function. The difference between the predicted μ of the reference chronology (R) and that of the test validation sample (S) ($\mu_R - \mu_S$) is a measure of dissimilarity in the year of 50% increase of the two curves, and hence age determination bias (Hamel *et al.* 2008; Kestelle *et al.* 2016). This means that if the validation sample birth years are estimated correctly (birth year = collection year – estimated age), the value of $\mu_R - \mu_S$ is zero. For the purposes of this model, a midpoint of otolith deposition for every sample must be used. Hence, the birth year of each test validation specimen was adjusted by +1 year to account for the 2-year core, and the Pacific halibut birth years were adjusted by +0.5 years to account for using whole otoliths from 1-year-old juveniles (Kestelle *et al.* 2016). Bayesian methods were used to fit the models using Markov chain Monte Carlo (MCMC) simulation (2 000 000 samples, burn-in = 1 000 000, thinned at 1000) and the converged posterior sample, $n = 1000$, was used to compute the probability of ageing bias. As presented in Kestelle *et al.* (2016) and summarised here, the MCMC probability density of $\mu_R - \mu_S$ is a measure of age determination bias. If the probability density is centred on zero, then the estimated ages of the specimens in the test validation sample can be considered accurate. An indication of bias in the estimated ages can be

^ANote: reference to trade names does not imply endorsement by the National Marine Fisheries Service, National Oceanic and Atmospheric Administration (NOAA).

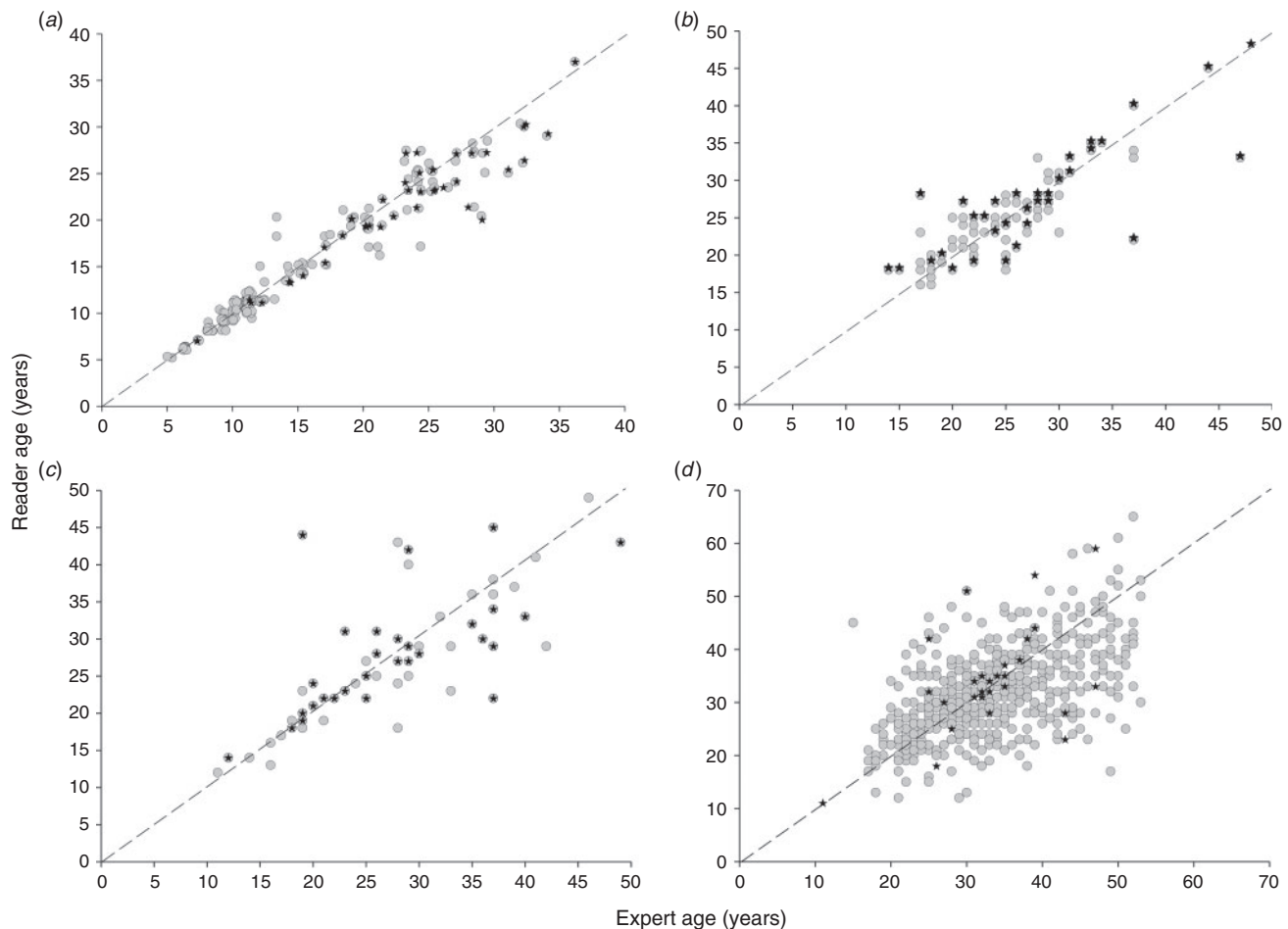


Fig. 3. Age bias plots (reader v. expert) for candidate samples (grey circles) and samples randomly chosen for ^{14}C analysis (black stars): (a) redstripe rockfish (*Sebastes proriger*), (b) harlequin rockfish (*Sebastes variegatus*), (c) shortspine thornyhead (*Sebastolobus alascanus*) and (d) shortraker rockfish (*Sebastes borealis*).

assessed by calculating the tail probability greater or less than zero; that is, $\text{Prob}[(\mu_R - \mu_S)] > 0$.

Results

Age determination and inter-reader precision

Ages estimated by six independent readers for harlequin rockfish test validation specimens spanned 14–87 years. The expert's age estimates spanned 14–66 years, resulting in predicted birth years from 1949 to 1982 (Table S1). Ages estimated by six independent readers for redstripe rockfish spanned 7–38 years. The expert's age estimates spanned 7–36 years, resulting in predicted birth years from 1945 to 1979 (Table S2). Age estimation of harlequin rockfish was more difficult than that of redstripe rockfish. This is demonstrated in percentage agreements of 47.6 and 51.35% for harlequin rockfish and redstripe rockfish respectively, differences in the other inter-reader precision statistics (Table S5) and by typical standard deviations of average ages from the six readers (Tables S1, S2). This difficulty was also noted subjectively by the expert age reader and may be related, in part, to the fact that age estimates for chosen harlequin

rockfish specimens were older on average (32.8 years; $n = 40$) than for chosen redstripe rockfish (22.7 years; $n = 41$). For redstripe rockfish, in specimens greater than ~20 years of age, the second reader's age estimates were biased low compared with the expert's age estimates (Fig. 3a). For harlequin rockfish, there was a bias between the expert's and second reader's age estimates; the reader's age estimates were more often higher than the expert's (Fig. 3b).

The shortraker rockfish and shortspine thornyhead specimens were only read twice, and the ages for each specimen were then averaged. In shortspine thornyhead specimens (by design, all specimens were ≥ 24 cm) the age estimates ranged from 12 to 49 years. The specimens' average age estimates ranged from 13 to 46 years (Table S3). The individual shortraker rockfish age estimates ranged from 11 to 59 years, and the specimens' averaged age estimates ranged from 11 to 53 years (Table S4). The 95% CIs around averaged age estimates for both shortspine thornyhead and shortraker rockfish were large, over 10 years when the two age estimates differed greatly. Hence, the CIs are not as informative compared with the other two species. The inter-reader percentage agreement for shortspine thornyhead and

Table 1. Estimated parameters for the coupled-function model using three datasets: Pacific halibut (*Hippoglossus stenolepis*) reference chronology, harlequin rockfish (*Sebastes variegatus*), and redstripe rockfish (*Sebastes proriger*)
CI, credibility interval

| Model parameter | Model attribute | Pacific halibut reference ($n = 36$) | | Harlequin rockfish ($n = 40$) | | Redstripe rockfish ($n = 41$) | |
|-----------------|-------------------------------------|--|----------------|---------------------------------|----------------|---------------------------------|----------------|
| | | Median | 95% CI | Median | 95% CI | Median | 95% CI |
| λ (‰) | Pre-bomb $\Delta^{14}\text{C}$ | -106.4 | -117.5, -96.3 | -99.7 | -160, -54.4 | -87.8 | -102.4, -73.2 |
| k (‰) | Absolute $\Delta^{14}\text{C}$ rise | 185.2 | 168.8, 201.9 | 240.5 | 139.4, 400.5 | 157.7 | 139.9, 174.8 |
| μ (year) | Year of 50% rise | 1963.1 | 1962.5, 1963.8 | 1967.2 | 1965.5, 1968.5 | 1963.9 | 1963.1, 1964.6 |
| σ | Pulse curve s.d. | 2.61 | 1.76, 3.52 | 3.314 | 0.641, 8.668 | 2.356 | 1.247, 3.399 |
| r (per year) | Decay rate | 0.004 | -0.015, 0.025 | 0.0569 | 0.0038, 0.1226 | 0 ^A | -0.101, 0.034 |
| σ_e^2 | Error variance | 343.7 | 190.2, 510.1 | 1936.9 | 1092.3, 2886.7 | 375.8 | 221.7, 565 |

^ANot different from 0, therefore not used in parameterisation.

shortraker rockfish was 21.21 and 5.58% respectively. The relative age determination difficulty is further reflected in other inter-reader precision statistics (Table S5). For shortspine thornyhead, agreement between reader and expert was generally good until ~ 20 years of age. Beyond the age of 20 years there was more variability between the two sets of ages, and a bias did exist (Fig. 3c). Low precision in shortspine thornyhead may have been partially a result of preferentially choosing otoliths from fish that were ≥ 24 cm, resulting in overall older age estimates (Table S3). For shortraker rockfish, there was a large variability in the reader's ages with respect to the expert's ages throughout the full range of ages. This variability in shortraker rockfish ages was larger compared with the other species, but there was no discernible bias between the two readers (Fig. 3d). The age readers indicated that age estimation of these two species was generally difficult, and confidence in age estimates was low.

$\Delta^{14}\text{C}$ analysis and age validation

Statistical inference of ageing bias is based on the properties of the model. We evaluated MCMC simulation performance by examining the posterior sample. Here the Bayesian model and MCMC simulation were computationally efficient, yielding 1000 samples with which to compute summary statistics and develop a framework to assess ageing bias. Initial testing of the MCMC simulation showed burn-in was achieved after 10 000 samples, and between-sample autocorrelation of estimated parameters was non-significant after a log of 10 sample parameter sets. We nevertheless discarded the first half of the 2 million samples and thinned at a rate of 1000. These results are shown in Fig. S1, which provides trace, autocorrelation and posterior density plots. The simulation traversed the parameter space efficiently, which is indicated by smooth unimodal posterior density, low autocorrelation and a large effective sample size.

Trends in the redstripe rockfish $\Delta^{14}\text{C}$ values (chronologies) were largely similar to the Pacific halibut reference chronology. Generally, in redstripe rockfish and the reference chronology, $\Delta^{14}\text{C}$ began to rise above pre-bomb levels shortly after the onset of aboveground nuclear testing in the late 1950s to early 1960s, after which $\Delta^{14}\text{C}$ increased more rapidly in the mid-1960s. The estimated model parameters of chronologies in redstripe rockfish and Pacific halibut reference were nearly identical (Table 1; Fig. 4a); $\Delta^{14}\text{C}$ in redstripe rockfish reached an asymptotic maximum around 1970, similar to the halibut reference, with a

total increase of 157.7‰. Here, the parameter of primary interest is μ , 50% of the $\Delta^{14}\text{C}$ rise; redstripe rockfish had a μ_S of 1963.9 and the Pacific halibut reference chronology's μ_R was 1963.1. In redstripe rockfish, the posterior distribution of $\mu_R - \mu_S$ was found at ~ -0.7 years, with an $\sim 85\%$ probability of being less than zero, indicating a mostly negative bias (underageing) of redstripe rockfish ages (Fig. 4a). However, there was only a $\sim 35\%$ probability of underageing by 1 year, an $\sim 5\%$ probability of underageing by ≥ 2 years and $< 5\%$ probability of overageing by ≥ 1 year.

Trends in the harlequin rockfish $\Delta^{14}\text{C}$ values (chronologies) were only somewhat similar to the Pacific halibut reference chronology, and indicated some notable age determination bias. The estimated model parameters and general shapes of chronologies in harlequin rockfish and Pacific halibut reference were similar (Table 1; Fig. 4b). Harlequin rockfish $\Delta^{14}\text{C}$ values had nearly the same pre-bomb values, reached approximately the same maximum (having a total increase of 240.5 v. 185.2 for Pacific halibut), but exhibited a post-peak decline after 1972. However, harlequin rockfish $\Delta^{14}\text{C}$ values were right-shifted compared with Pacific halibut, representing a delay in rise of several years with a μ_S at 1967.2. The $\mu_R - \mu_S$ between the harlequin and the Pacific halibut reference chronologies was found at ~ -3.8 years, and indicated a 100% probability of a negative bias, or that underageing by ~ 3 or 4 years was most probable. However, there was only an $\sim 5\%$ probability of an underageing bias > 5 years.

The coupled function was not fit to the measured $\Delta^{14}\text{C}$ values in shortspine thornyhead or shortraker rockfish otoliths. Neither of these two test species exhibited a trend similar to the Pacific halibut reference chronology; hence, the models (parameter estimation) did not converge (Fig. 4c, d). Their $\Delta^{14}\text{C}$ values were all scattered low and to the right of the Pacific halibut reference chronology. The Bayesian model and MCMC simulations did not converge to estimate parameter sets. Therefore, we were unable to derive an estimate of ageing bias from the $\Delta^{14}\text{C}$ values in either shortspine thornyhead or shortraker rockfish. In both these species, there appeared to be an ~ 10 -year delay in the start of the bomb-produced increase (Fig. 4c, d). The shortspine thornyhead $\Delta^{14}\text{C}$ values ranged from ~ -150 to 0‰, and the pre-bomb values were clustered around 130‰. The shortraker rockfish $\Delta^{14}\text{C}$ values ranged from ~ -175 to 60‰, with pre-bomb $\Delta^{14}\text{C}$ values clustered around -150 ‰. Both species did not appear to

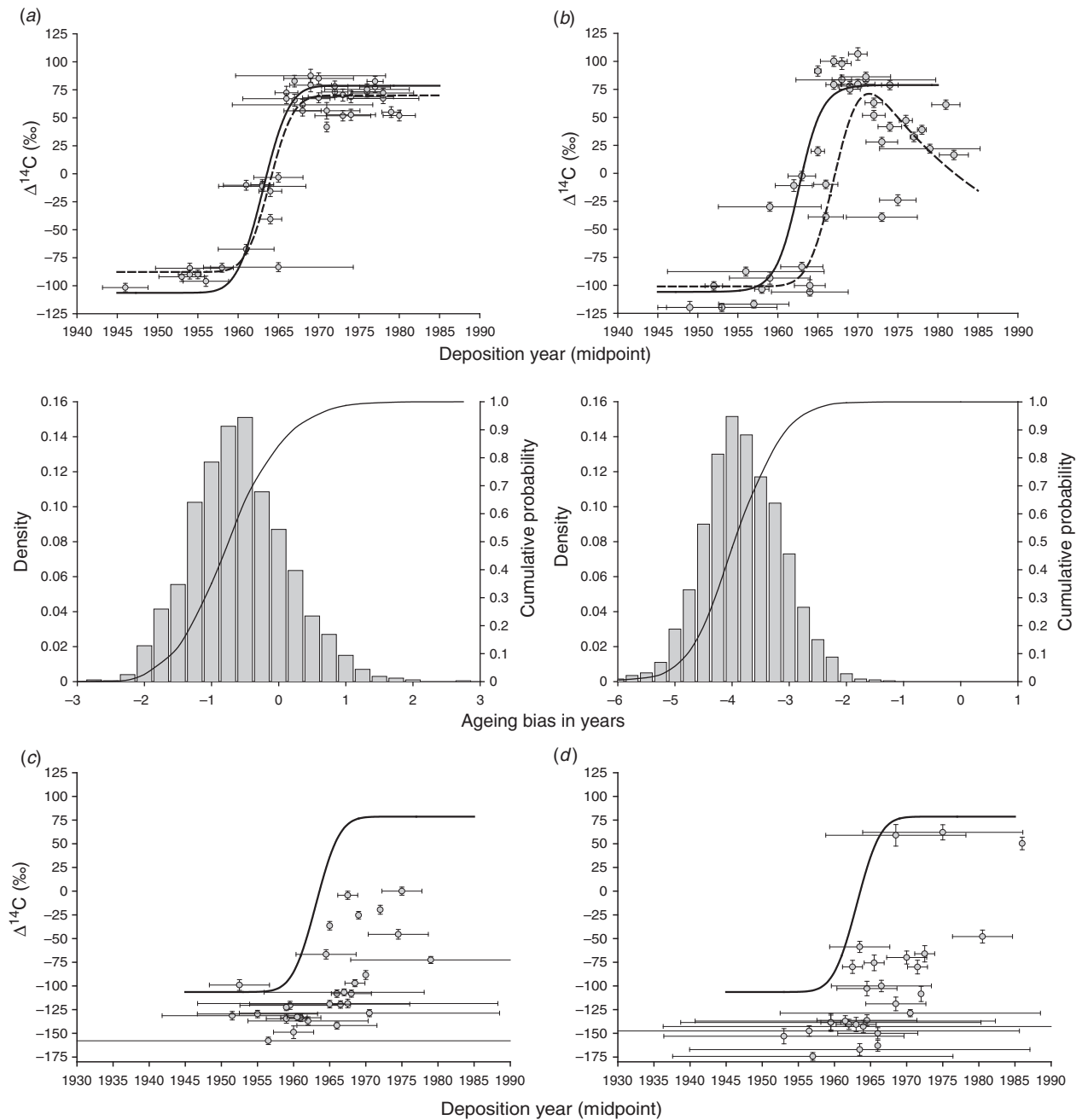


Fig. 4. (a, b) Validation specimen $\Delta^{14}\text{C}$ pulse curves (chronologies; dashed lines and points) compared to the Pacific halibut (*Hippoglossus stenolepis*) $\Delta^{14}\text{C}$ reference pulse curve (chronology; solid line) and the resulting Markov chain Monte Carlo (MCMC) probability density of ageing bias, $\mu_R - \mu_S$ for (a) redstripe rockfish (*Sebastes proriger*) and (b) harlequin rockfish (*Sebastes variegatus*). Validation specimen $\Delta^{14}\text{C}$ data points compared to the Pacific halibut $\Delta^{14}\text{C}$ reference chronology for (c) shortspine thornyhead (*Sebastolobus alascanus*) and (d) shorttraker rockfish (*Sebastes borealis*). Error bars are 95% confidence intervals.

have well-defined upper asymptotes. Without a fit model, little can be concluded about the accuracy of the estimated ages. All nine difficult-to-age shorttraker rockfish specimens had $\Delta^{14}\text{C}$ values in the extreme upper or lower range; that is, in the range of the expected upper and lower asymptotes. Therefore, because the $\Delta^{14}\text{C}$ values were not in an informative range, it was not even possible to subjectively evaluate the accuracy of estimated ages.

Discussion

Our age validation of redstripe rockfish was successful. The estimated ages appeared to be close to accurate, with the most probable age determination bias being only ~ 0.7 years less than true age (Fig. 4a). Hence, only minor revision, if any, in the age determination methods should be made. An age validation and estimated ageing bias for redstripe rockfish did not exist

previously. Therefore, this study is the first to independently confirm age estimates of redstripe rockfish, with a maximum validated age of 36 years. Maximum estimated ages of 46 and 55 years have been reported previously for this species from the Gulf of Alaska (Alaska Fisheries Science Center 2017) and British Columbia (Munk 2001) waters respectively. Although it is generally not appropriate to extrapolate beyond those in the study, these previous studies used age determination methodology similar to ours and therefore it could be reasonably assumed that their reported maximum ages are also accurate.

Our results, relative to the first study goal, indicate that current age determination practices for harlequin rockfish do not yield accurate estimates of age. Our second goal of estimating the probability of age reading bias was attained; it was highly probable ($\sim 95\%$) that an underageing bias of ~ 3 or 4 years exists in the harlequin rockfish samples (Fig. 4b). Therefore, our results can be used to revise and improve otolith preparation methods and age determination criteria for harlequin rockfish. The maximum age reported previously for harlequin rockfish is 76 years (Alaska Fisheries Science Center 2017), and the maximum age estimated by the expert reader in the present study was 75 years. Therefore, given the probable negative bias, this represents a new maximum age estimate, which is vital information for estimating natural mortality rates and other vital rates. There are two harlequin rockfish samples that appear as outliers (underaged), with deposition years of 1972 and 1974 (Fig. 4b). In our processing of these samples they appeared normal for this species and, hence, probably represent real variation. If these two samples were left out of the analysis, the estimated bias would be less.

Rockfish age determination is generally difficult, and there are several possible explanations for the observed small negative bias in redstripe rockfish and larger bias in harlequin rockfish age estimates (McCurdy *et al.* 2002; Goetz *et al.* 2012a). The earliest one to three annuli in rockfish otoliths are often the most difficult to interpret, especially if the otolith was not cut directly through its core during preparation. Compact annuli near the otolith's edge can also be challenging to interpret. Diffuse or faint growth patterns can occur within an otolith on even the clearest reading axis due to the degree of burning applied and to fading over time after preparation (McCurdy *et al.* 2002). In the future, great care should be made to interpret fine and compact growth zones in these areas. These issues may be especially true for harlequin rockfish, which were generally more difficult to age as indicated by lower inter-reader precision. Once refinements to the age determination methods are made, further independent confirmation of the ages should be done, especially the first year's growth zone interpretation (Stuart and McKillup 2002; Guido *et al.* 2004). The best precision is achieved by careful preparation of the otolith and calibration of ageing criteria between readers, especially with regard to interpretation of early growth zones. Goetz *et al.* (2012b) give some suggestions on cutting through the core and burning Scorpaenid otoliths. After revised methods and new criteria are developed, previously aged specimens can be re-aged and comparisons to the first ages made.

Our conclusions on redstripe rockfish and harlequin rockfish rely on the main assumption for this type of age validation study, that of an environmental and biological similarity between the

test validation and reference species. This means that in the absence of ageing error, the timing and magnitude of the ^{14}C increase should be similar in both the reference chronology and validation specimens. The importance of this assumption has been demonstrated in previous bomb-produced ^{14}C age validation studies by Kalish (1995), Campana and Jones (1998), Haltuch *et al.* (2013), Helser *et al.* (2014) and Wischniowski *et al.* (2015). The similarities of the redstripe rockfish and Pacific halibut pulse curves in the parameters we estimated, not only μ , is notable (Fig. 4a; Table 1). The observed pre-bomb values of $\Delta^{14}\text{C}$ in harlequin rockfish were nearly the same as in Pacific halibut, rising to a similar maximum and then decreasing; the Pacific halibut pulse curve does not show a decrease (Fig. 4b; Table 1). Our definition of bias uses μ ; however, consideration of σ , which defines the slope of the pulse curve, is important. If the validation and reference curves had estimates of σ that were different, this could be an indication of environmental and biological differences in the rate of ^{14}C uptake. This was not the case in our validation and reference curves (Fig. 4a, b; Table 1). Pacific halibut are well known to inhabit nearshore areas as juveniles, migrating deeper as they reach maturity (Norcross *et al.* 1996, 1999; Abookire *et al.* 2001). Redstripe and harlequin rockfish are less researched than halibut, but are also thought to inhabit nearshore areas as juveniles, the time period corresponding to the ^{14}C measured in the otolith cores (Gunderson and Sample 1980; Love *et al.* 2002). Further, the samples of these three species were all collected from same oceanic basin, the Gulf of Alaska. Therefore, they would all be expected to encounter generally similar concentrations of bomb-produced ^{14}C before ontogenetic migrations to deeper water. Small regional differences in conditions, such as nearshore water column mixing or less continental freshwater input, could conceivably cause a post-peak decline, as noted for the harlequin rockfish. However, the similarities between Pacific halibut and harlequin rockfish in other parameters (σ , k and λ) suggest that the main assumption was met in our comparisons. In situations where the assumption of environmental and biological similarities between a correctly aged test validation species and reference species is clearly not met, the differences between the pulse curves are greater (Campana and Jones 1998; Haltuch *et al.* 2013; Wischniowski *et al.* 2015).

Our results for shortspine thornyhead and shorttraker rockfish are inconclusive. The $\Delta^{14}\text{C}$ measured in otolith cores from both these species did not display the form of an expected pulse curve; the values were scattered below and to the right of the reference chronology. Therefore, the coupled-function model did not describe the $\Delta^{14}\text{C}$ values, and we did not attempt to fit this model to these data. Consequently, the estimated fish ages could not be validated and the probability density of $\mu_R - \mu_S$ was not estimated. The shorttraker rockfish had a special sample selection protocol, a set with clear ages and a set of difficult-to-age samples. Of the nine difficult-to-age samples, two had $\Delta^{14}\text{C}$ values slightly below but near the expected upper asymptote. The remaining seven samples had some of the lowest resulting $\Delta^{14}\text{C}$ values, ~ 50 ppm below the lower asymptote of the Pacific halibut reference chronology. Our hope was that when these nine $\Delta^{14}\text{C}$ values were plotted against the average age and compared to the values of the reference chronology (in the era of increasing $\Delta^{14}\text{C}$), an indication of the correct age would be clear. Unfortunately, this

was not the case. In our study the estimated maximum age of shortspine thornyhead and shortraker rockfish was 49 and 59 years respectively from specimens chosen to coincide with the era of increasing bomb-produced $\Delta^{14}\text{C}$, not the maximum age available. Maximum ages reported elsewhere are up to 89 and 157 years for shortspine thornyhead and shortraker rockfish respectively (Munk 2001; Alaska Fisheries Science Center 2017). Using radiometric age validation, ages older than observed in this study were confirmed as generally accurate for both species (Kline 1996; Kestelle *et al.* 2000; Hutchinson *et al.* 2007).

There are two possible explanations for the low and delayed $\Delta^{14}\text{C}$ in shortspine thornyhead and shortraker rockfish. First, in comparing these two species to Pacific halibut, the assumption that they are biologically and environmentally similar may not hold true. Shortraker rockfish and shortspine thornyhead are both known to often inhabit waters deeper than 400 m during their benthic juvenile stages (Jacobson and Vetter 1996; Orlov 2001). Juvenile Pacific halibut usually become benthic at depths less than 120 m (Norcross *et al.* 1996, 1999; International Pacific Halibut Commission 1998; Abookire *et al.* 2001). This distinction in depths occupied by these rockfish and Pacific halibut during their early life histories may violate the main assumption of environmental and biological similarity due to depth-related differences in oceanic mixing of ^{14}C . Following the period of atomic bomb testing, ocean surface water largely received bomb-produced ^{14}C through exchange at the air–sea interface. Below the mixed surface layer, the input rate of ^{14}C is reduced due to a lengthened mixing process from the surface, and by the influence of deep, ^{14}C -depleted water (Nydal 1993; Kumamoto *et al.* 2013). Thus, in shortspine thornyhead and shortraker rockfish, the low initial level and delayed increase of $\Delta^{14}\text{C}$ may be explained by the differences in depths occupied by the test validation and reference specimens. A delay in the $\Delta^{14}\text{C}$ pulse curve has also been seen in other species that are influenced by deeper water from below the mixed layer (Haltuch *et al.* 2013). Second, it is possible that both these species were underaged, but these results are not useful as an indicator of this. Previous radiometric age validations indicate that shortraker rockfish and shortspine thornyhead can both reach old ages, and in some cases underageing can occur (Kline 1996; Kestelle *et al.* 2000; Hutchinson *et al.* 2007). The possibility of underageing cannot be ignored given the difficulties of age determination in these two species. The age determination problems described previously in this paper, regarding the earliest years and the growth zones on the otolith's edge, are pertinent to the question of underageing of shortspine thornyhead and shortraker rockfish. In addition, shortspine thornyhead otoliths occasionally have faint growth zones among those posited to form annually. This was especially true in otolith regions representing fish growth before maturity, which is common in rockfish species (Goetz *et al.* 2012a), but also occurred in otolith regions representing adult life history, which is less common among other rockfish species. The interpretation of these faint growth zones in shortspine thornyhead is a source of poor accuracy and low precision because otolith readers must make subjective decisions as to their annual nature. These areas could be a source of underageing if the growth zones are more compact and fine than previously thought. This makes shortspine thornyhead unique compared with other rockfish species aged at the AFSC. Both shortspine thornyhead and shortraker rockfish were aged by

otolith thin sectioning, instead of the break-and-burn method, due to these age reading difficulties. Importantly, these two explanations, the unmet assumption and underageing, are completely confounded and cannot be separated.

This validation study successfully demonstrated the level of accuracy in estimated ages of redstripe and harlequin rockfish. This was useful because it indicates that future revisions are necessary in applying age determination criteria to harlequin rockfish. The interpretation of the first two or three annuli and of the seasonal growth on the otolith's edge are the most likely areas for revisions, especially for harlequin rockfish. The results here will help in using age data in stock assessments of these two species. Results for shortspine thornyhead and shortraker rockfish were inconclusive, indicating that the Pacific halibut reference was not biologically or environmentally appropriate for an age validation of these species or that underageing occurred. The marked difference in outcomes between these four species highlights the importance of using the correct known-age reference chronology. Future sampling of $\Delta^{14}\text{C}$ in shortspine thornyhead and shortraker rockfish otoliths to estimate an upper asymptote, using specimens with estimated birth years in the range 1980–2000s, could help separate these two possibilities.

This study is unique in the fact that two different habitat preferences are represented by four species. Further, the study was unique in that the sample size for each species was far larger than most other single-species age validation studies, lending more confidence to the results. In addition, using the MCMC probability densities to estimate age determination bias is unique among many previous age validation studies.

Conflicts of interest

The authors declare that they have no conflicts of interest.

Declaration of funding

This study was funded by the North Pacific Research Board (Project #1401).

Acknowledgments

The authors thank Paul Spencer of the Alaska Fisheries Science Center (AFSC) for early insights into this study, staff in the Age and Growth Program at the AFSC for support while doing this project and Beth Matta of the AFSC for very useful comments and edits that improved early versions of this manuscript. For reviewing and commenting on this manuscript, the authors further thank Cindy Tribuzio and Paul Spencer.

References

- Abookire, A. A., Piatt, J. F., and Norcross, B. L. (2001). Juvenile groundfish habitat in Kachemak Bay, Alaska, during late summer. *Alaska Fishery Research Bulletin* 8(1), 45–56.
- Alaska Fisheries Science Center (2017). Fish species maximum age data. Available at <https://www.fisheries.noaa.gov/alaska/commercial-fishing/fish-species-maximum-age-data> [Verified 15 November 2019].
- Andrews, A. H., Kalish, J. M., Newman, S. J., and Johnston, J. M. (2011). Bomb radiocarbon dating of three important reef-fish species using Indo-Pacific $\Delta^{14}\text{C}$ chronologies. *Marine and Freshwater Research* 62(11), 1259–1269. doi:10.1071/MF11080
- Beamish, R. J. (1979). New information on the longevity of Pacific ocean perch (*Sebastes alutus*). *Journal of the Fisheries Research Board of Canada* 36(11), 1395–1400. doi:10.1139/F79-199

- Beamish, R. J., and Fournier, D. A. (1981). A method for comparing the precision of a set of age determinations. *Canadian Journal of Fisheries and Aquatic Sciences* **38**(8), 982–983. doi:10.1139/F81-132
- Beamish, R. J., and McFarlane, G. A. (1983). The forgotten requirement for age validation in fisheries biology. *Transactions of the American Fisheries Society* **112**(6), 735–743. doi:10.1577/1548-8659(1983)112<735:TFRFAV>2.0.CO;2
- Butler, J. L., Kestelle, C., Rubin, K., Kline, D. E., Heijnis, H., Jacobson, L., Andrews, A., and Wakefield, W. W. (1995). Age determination of shortspine thornyhead *Sebastes alascanus*, using otolith sections and ^{210}Pb : ^{226}Ra ratios. Administrative Report LJ-95-12, National Marine Fisheries Service, Southwest Fisheries Science Center, La Jolla, CA, USA.
- Campana, S. E. (2001). Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *Journal of Fish Biology* **59**(2), 197–242. doi:10.1111/J.1095-8649.2001.TB00127.X
- Campana, S. E., and Jones, C. M. (1998). Radiocarbon from nuclear testing applied to age validation of black drum, *Pogonias cromis*. *Fishery Bulletin* **96**(2), 185–192.
- Campana, S. E., Annand, M. C., and McMillan, J. I. (1995). Graphical and statistical methods for determining the consistency of age determinations. *Transactions of the American Fisheries Society* **124**(1), 131–138. doi:10.1577/1548-8659(1995)124<0131:GASMF>2.3.CO;2
- Chang, W. Y. B. (1982). A statistical method for evaluating the reproducibility of age determination. *Canadian Journal of Fisheries and Aquatic Sciences* **39**(8), 1208–1210. doi:10.1139/F82-158
- Echave, K. B., and Hulson, P. F. (2018). Assessment of the thornyhead stock complex in the Gulf of Alaska. Available at <https://www.afsc.noaa.gov/REFM/Docs/2018/GOA/GOAthorny.pdf> [Verified 14 November 2019].
- Fissel, B., Dalton, M., Garber-Yonts, B., Haynie, A., Kasperski, S., Lee, J., Lew, D., Lavoie, A., Seung, C., Sparks, K., Szymkowiak, M., and Wise, S. (2019). Stock assessment and fishery evaluation report for the groundfish fisheries of the Gulf of Alaska and Bering Sea/Aleutian Islands area: economic status of the groundfish fisheries off Alaska, 2017. Available at <https://www.fisheries.noaa.gov/webdam/download/90070908> [Verified 15 November 2019].
- Goetz, B. J., Pistion, C. E., and Gburski, C. M. (2012a). Rockfish (*Sebastes*) species. In 'Age Determination Manual of the Alaska Fisheries Science Center Age and Growth Program'. (Eds M. E. Matta and D. K. Kimura.) NOAA Professional Paper NMFS 13, pp. 49–64. (National Marine Fisheries Service: Seattle, WA, USA.)
- Goetz, B. J., Piston, C. E., Hutchinson, C. E., Johnson, C. G., and Matta, M. E. (2012b). Collection and preparation of otoliths for age determination. In 'Age Determination Manual of the Alaska Fisheries Science Center Age and Growth Program'. (Eds M. E. Matta and D. K. Kimura.) NOAA Professional Paper NMFS 13, pp. 11–15. (National Marine Fisheries Service: Seattle, WA, USA.)
- Guido, P., Omori, M., Katayama, S., and Kimura, K. (2004). Classification of juvenile rockfish, *Sebastes inermis*, to *Zostera* and *Sargassum* beds, using the macrostructure and chemistry of otoliths. *Marine Biology* **145**(6), 1243–1255. doi:10.1007/S00227-004-1402-Y
- Gunderson, D. R., and Sample, T. M. (1980). Distribution and abundance of rockfish off Washington, Oregon, and California during 1977. *Marine Fisheries Review* **42**(3–4), 2–16.
- Haltuch, M. A., Hamel, O. S., Piner, K. R., McDonald, P., Kestelle, C. R., and Field, J. C. (2013). A California current bomb radiocarbon reference chronology and petrale sole (*Eopsetta jordani*) age validation. *Canadian Journal of Fisheries and Aquatic Sciences* **70**(1), 22–31. doi:10.1139/CJFAS-2011-0504
- Hamel, O. S., Piner, K. R., and Wallace, J. R. (2008). A robust deterministic model describing the bomb radiocarbon signal for use in fish age validation. *Transactions of the American Fisheries Society* **137**(3), 852–859. doi:10.1577/T07-144.1
- Helser, T. E., Kestelle, C. R., and Lai, H. L. (2014). Modeling environmental factors affecting assimilation of bomb-produced $\Delta^{14}\text{C}$ in the North Pacific Ocean: Implications for age validation studies. *Ecological Modelling* **277**, 108–118. doi:10.1016/J.ECOLMODEL.2014.01.011
- Hutchinson, C. E., Kestelle, C. R., Kimura, D. K., and Gunderson, D. R. (2007). Using radiometric ages to develop conventional ageing methods for shorttraker rockfish (*Sebastes borealis*). In 'Biology, Assessment, and Management of North Pacific Rockfishes'. (Eds J. Heifetz, J. DiCosimo, A. J. Gharrett, M. S. Love, V. M. O'Connell, and R. D. Stanley.) pp. 237–249. (Alaska Sea Grant, University of Alaska Fairbanks: Anchorage, AK, USA.)
- International Pacific Halibut Commission (1998). The Pacific halibut: biology, fishery, and management. Technical Report number 40, International Pacific Halibut Commission, Seattle, WA, USA.
- Jacobson, L. D., and Vetter, R. D. (1996). Bathymetric demography and niche separation of thornyhead rockfish: *Sebastes alascanus* and *Sebastes altivelis*. *Canadian Journal of Fisheries and Aquatic Sciences* **53**(3), 600–609. doi:10.1139/F95-207A
- Kalish, J. M. (1995). Radiocarbon and fish biology. In 'Recent Developments in Fish Otolith Research'. (Eds D. H. Secor, J. M. Dean, and S. E. Campana.) pp. 637–653. (University of South Carolina Press: Columbia, SC, USA.)
- Kestelle, C. R., Kimura, D. K., and Jay, S. R. (2000). Using Pb-210/Ra-226 disequilibrium to validate conventional ages in Scorpaenids (genera *Sebastes* and *Sebastes*). *Fisheries Research* **46**(1–3), 299–312. doi:10.1016/S0165-7836(00)00155-7
- Kestelle, C. R., Kimura, D. K., and Goetz, B. J. (2008). Bomb radiocarbon age validation of Pacific ocean perch (*Sebastes alutus*) using new statistical methods. *Canadian Journal of Fisheries and Aquatic Sciences* **65**(6), 1101–1112. doi:10.1139/F08-038
- Kestelle, C. R., Helser, T. E., Wischniowski, S. G., Loher, T., Goetz, B. J., and Kautzi, L. A. (2016). Incorporation of bomb-produced ^{14}C into fish otoliths: a novel approach for evaluating age validation and bias with an application to yellowfin sole and northern rockfish. *Ecological Modelling* **320**, 79–91. doi:10.1016/J.ECOLMODEL.2015.09.013
- Kestelle, C. R., Helser, T. E., McKay, J. L., Johnston, C. G., Anderl, D. M., Matta, M. E., and Nichol, D. G. (2017). Age validation of Pacific cod (*Gadus macrocephalus*) using high-resolution stable oxygen isotope ($\delta^{18}\text{O}$) chronologies in otoliths. *Fisheries Research* **185**, 43–53. doi:10.1016/J.FISHRES.2016.09.024
- Kerr, L. A., Andrews, A. H., Munk, K., Coale, K. H., Frantz, B. R., Cailliet, G. M., and Brown, T. A. (2005). Age validation of quillback rockfish (*Sebastes maliger*) using bomb radiocarbon. *Fishery Bulletin* **103**(1), 97–107.
- Kimura, D. K., and Anderl, D. M. (2005). Quality control of age data at the Alaska Fisheries Science Center. *Marine and Freshwater Research* **56**(5), 783–789. doi:10.1071/MF04141
- Kimura, D. K., Kestelle, C. R., Goetz, B. J., Gburski, C. M., and Buslov, A. V. (2006). Corroborating the ages of walleye pollock (*Theragra chalcogramma*). *Marine and Freshwater Research* **57**(3), 323–332. doi:10.1071/MF05132
- Kline, D. E. (1996). Radiochemical age verification for two deep-sea rockfishes. M.Sc. Thesis, San Jose State University, San Jose, CA, USA.
- Kumamoto, Y., Murata, A., Kawano, T., Watanabe, S., and Fukasawa, M. (2013). Decadal changes in bomb-produced radiocarbon in the Pacific Ocean from the 1990s to 2000s. *Radiocarbon* **55**(3), 1641–1650. doi:10.1017/S003822200048554
- Love, M. S., Yoklavich, M., and Thorsteinson, L. (2002). 'The Rockfishes of the Northeast Pacific.' (University of California Press: Berkeley, CA, USA.)
- Matta, M. E., and Kimura, D. K. (2012). Age determination manual of the Alaska Fisheries Science Center Age and Growth Program. NOAA, Professional Paper NMFS 13, United States Department of Commerce, Seattle, WA, USA.

- McCurdy, W. M., Panfili, J., Meunier, A. J., Geffen, A. J., and de Pontual, H. (2002). Preparation of calcified structures. In 'Manual of Fish Sclerochronology'. (Eds J. Panfili, H. de Pontual, H. Troadec, and P. J. Wright.) pp. 331–357. (Ifremer–IRD Coedition: Brest, France.)
- Munk, K. M. (2001). Maximum ages of groundfishes in waters off Alaska and British Columbia and considerations of age determination. *Alaska Fishery Research Bulletin* **8**(1), 12–21.
- Norcross, B. L., Holladay, B. A., Dressel, S. C., and Frandsen, M. (1996). Recruitment of juvenile flatfishes in Alaska: habitat preference near Kodiak Island. OCS Study MMS 96-0003, University of Alaska, Coastal Marine Institute, Fairbanks, AK, USA.
- Norcross, B. L., Blanchard, A., and Holladay, B. A. (1999). Comparison of models for defining nearshore flatfish nursery areas in Alaskan waters. *Fisheries Oceanography* **8**(1), 50–67. doi:10.1046/J.1365-2419.1999.00087.X
- Nydal, R. (1993). Application of bomb ^{14}C as a tracer in the global carbon cycle. *Trends in Geophysical Research* **2**, 355–364.
- Orlov, A. M. (2001). Ocean current patterns and aspects of life history of some northwestern Pacific scorpaenids. In 'Spatial Processes and Management of Marine Populations'. (Eds G. H. Kruse, N. Bez, A. Booth, M. W. Dorn, S. Hills, R. N. Lipcius, D. Pelletier, C. Roy, S. J. Smith, and D. Witherell.) pp. 161–184. (University of Alaska Fairbanks: Fairbanks, AK, USA.)
- Parker, S. J., Berkeley, S. A., Golden, J. T., Gunderson, D. R., Heifetz, J., Hixon, M. A., Larson, R., Leaman, B. M., Love, M. S., Musick, J. A., O'Connell, V. M., Ralston, S., Weeks, H. J., and Yoklavich, M. M. (2000). Management of Pacific rockfish. *Fisheries (Bethesda, Md.)* **25**(3), 22–30. doi:10.1577/1548-8446(2000)025<0022:MOPR>2.0.CO;2
- Pearson, K. E., and Gunderson, D. R. (2003). Reproductive biology and ecology of shortspine thornyhead rockfish, *Sebastolobus alascanus*, and longspine thornyhead rockfish, *S. altivelis*, from the northeastern Pacific Ocean. *Environmental Biology of Fishes* **67**(2), 117–136. doi:10.1023/A:1025623426858
- Piner, K. R., and Wischniowski, S. G. (2004). Pacific halibut chronology of bomb radiocarbon in otoliths from 1944 to 1981 and a validation of ageing methods. *Journal of Fish Biology* **64**(4), 1060–1071. doi:10.1111/J.1095-8649.2004.0371.X
- Rooper, C. N. (2008). An ecological analysis of rockfish (*Sebastes* spp.) assemblages in the North Pacific Ocean along broad-scale environmental gradients. *Fishery Bulletin* **106**(1), 1–11.
- Stuart, I. G., and McKillup, S. C. (2002). The use of sectioned otoliths to age barramundi (*Lates calcarifer*) (Bloch, 1790). *Hydrobiologia* **479**(1–3), 231–236. doi:10.1023/A:1021021720945
- Stuiver, M., and Polach, H. A. (1977). Discussion: reporting of ^{14}C data. *Radiocarbon* **19**(3), 355–363. doi:10.1017/S0033822200003672
- Tribuzio, C. A., Coutré, K., and Echave, K. B. (2017). Assessment of the other rockfish stock complex in the Gulf of Alaska. Available at <https://www.afsc.noaa.gov/REFM/Docs/2017/GOAorock.pdf> [Verified 15 November 2019].
- Wischniowski, S. G., Kestelle, C. R., Loher, T., and Helser, T. E. (2015). Incorporation of bomb-produced C-14 into fish otoliths: an example of basin-specific rates from the North Pacific Ocean. *Canadian Journal of Fisheries and Aquatic Sciences* **72**(6), 879–892. doi:10.1139/CJFAS-2014-0225
- Woods Hole Oceanographic Institution National Ocean Sciences Accelerator Mass Spectrometry Facility (2018). Radiocarbon data & calculations. Available at <http://www.whoi.edu/nosams/page.do?pid=40146> [Verified 15 November 2019].

Handling Editor: Peter Unmack