

Bomb radiocarbon dating of the endangered white abalone (*Haliotis sorenseni*): investigations of age, growth and lifespan

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Abstract. Understanding basic life-history characteristics of white abalone (*Haliotis sorenseni*), such as estimated lifespan, is critical to making informed decisions regarding the recovery of this endangered species. All predictive modelling tools used to forecast the status and health of populations following restoration activities depend on a validated estimate of adult lifespan. Of the seven *Haliotis* species in California, white abalone is considered to have the highest extinction risk and was the first marine invertebrate listed as an endangered species under the Federal *Endangered Species Act* (ESA). Lifespan was previously estimated from observations of early growth; however, no study has generated ages for the largest white abalone. To address questions of age and growth, bomb radiocarbon ($\Delta^{14}\text{C}$) dating was used on shells from large white abalone. Measured bomb $\Delta^{14}\text{C}$ levels were compared to regional $\Delta^{14}\text{C}$ reference records to provide estimates of age, growth and lifespan. Bomb radiocarbon dating indicated that growth was variable among individuals, with a maximum estimated age of 27 years. The findings presented here provide support for previous age and growth estimates and an estimated lifespan near 30 years. These age data support the perception of a critical need for restoring the remnant aging and potentially senescent population.

Additional keywords: age validation, carbon-14, Haliotidae, longevity, Mollusca, Southern California Bight.

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Introduction

Abalone (*Haliotis* spp.) of the north-eastern Pacific Ocean have suffered severe population declines that have been primarily attributed to commercial and recreational fishing (Karpov *et al.* 2000; Rogers-Bennett *et al.* 2002), and disease, poaching and predation have exacerbated the decline (Daniels and Floren 1998; Watson 2000; Moore *et al.* 2002). Efforts to manage abalone in California have relied on estimating current levels of density in the wild, comparing current-day values to those estimated before population collapse, and carrying out actions that serve to restore densities to pre-exploitation levels. The predictive value of models used to determine outcomes of

different restoration scenarios increases if validated estimates of key demographic variables, such as lifespan and expected survival rates, can be incorporated into the models (Tegner *et al.* 1989; Rogers-Bennett and Leaf 2006; Leaf *et al.* 2008b). Obtaining this kind of information for endangered populations is challenging because of their rarity and elusive nature, research permitting requirements, and the pressure of destructive sampling. In this case, the use of archived museum materials was invaluable (Suarez and Tsutsui 2004).

Of the seven *Haliotis* species in California, white abalone (*Haliotis sorenseni*) is considered at highest risk of extinction, with current estimates of population size less than 1% of historic

estimates (Rogers-Bennett *et al.* 2002), and continue to decline in the absence of fishing (Butler *et al.* 2006; Stierhoff *et al.* 2012). In 2001, the species became the first marine invertebrate to be included on the endangered species list under the Federal *Endangered Species Act* (ESA). As a result of this listing, a recovery plan was drafted to guide efforts for rebuilding white abalone populations (National Marine Fisheries Service 2008). An understanding of white abalone life-history characteristics is critical to restoring the species from its extirpated state and will be necessary for post-recovery management. Although much of the ecology of white abalone has been described (Tutschulte 1976), age and growth relationships and the maximum lifespan are poorly understood. Given the large shell-size of extant populations, and the uncertainty of reproductive potential from large and potentially old individuals, it has been hypothesised that remaining individuals are near the end of their lifespan and may have little or no reproductive potential (Davis *et al.* 1996; Hobday and Tegner 2000). This hypothesis is supported by 14% per year declines documented in the remnant wild white abalone populations (Stierhoff *et al.* 2012).

Estimates of age, growth and lifespan for white abalone are limited to studies of early growth and growth in captivity. Limited observations in the field and captive environments indicate that early growth is initially rapid, slows with increasing size, and is variable among individuals (Tutschulte and Connell 1988). From those observations, an age near maximum size (~210-mm maximum shell length, MSL) was extrapolated to ~35 years; however, the estimates of age and growth remain unconfirmed past an age of ~10 years and lifespan is not known. No study has generated ages for large adult white abalone. For a better understanding of ontogenetic growth, it is important to evaluate as much of the lifespan as possible (Beamish and McFarlane 1983). Because mollusk shell provides a conserved carbonate record that covers the lifespan of any given individual (Richardson 2000), there is promise for the use of bomb radiocarbon dating as an independent measure of age for white abalone beyond 10 years of age (e.g. Weidman and Jones 1993).

Bomb radiocarbon dating is a technique that has evolved as a unique application for validating the age of fishes and invertebrates. The approach relies on a conserved record of the rapid increase in radiocarbon (^{14}C) that occurred in the oceans of the world as a result of atmospheric testing of thermonuclear devices in the 1950s and 1960s (Broecker and Peng 1982). The marine signal is delayed relative to the atmospheric signal by 7–10 years (Nydal 2000), but the uptake of bomb-produced radiocarbon by the marine environment was virtually synchronous in the mixed layer of mid-latitude oceans (Broecker and Peng 1982). For marine carbonates, this signal was first recorded as a time series in hermatypic corals (Druffel and Linick 1978). This time-specific signal provides a reference point that can be used to determine age. Application to fishes began with an innovative comparison of $\Delta^{14}\text{C}$ values recorded in otolith (fish ear bone) carbonate relative to regional $\Delta^{14}\text{C}$ records from hermatypic corals (Kalish 1993). Measured $\Delta^{14}\text{C}$ levels provided an independent determination of age for corroboration of age estimates from growth-zone counting in otoliths (Campana 2001, Kalish 2001). Bomb radiocarbon dating has since been applied successfully to numerous teleost fishes by using otoliths (e.g. Andrews *et al.* 2007; Ewing *et al.* 2007; Neilson and

Campana 2008) and has been expanded to other marine organisms (e.g. Ebert and Southon 2003; Frantz *et al.* 2005; Roark *et al.* 2006; Stewart *et al.* 2006), including mollusks (e.g. Weidman and Jones 1993; Kilada *et al.* 2009). In addition, recent bomb radiocarbon work with red abalone (*H. rufescens*) has shown that abalone shell can serve as a record of the $\Delta^{14}\text{C}$ signal in the north-eastern Pacific Ocean (Leaf *et al.* 2008a).

The aim of the present study was to use bomb radiocarbon dating to provide estimates of age and growth for white abalone. It was hypothesised that bomb radiocarbon dating can provide age estimates for the largest shells because of the typically time-specific nature of the rise of $\Delta^{14}\text{C}$. To test the applicability of the technique relative to other regional $\Delta^{14}\text{C}$ reference records, $\Delta^{14}\text{C}$ measurements were also made from shell material with known collection dates. It was further hypothesised that the compiled regional $\Delta^{14}\text{C}$ reference information will provide valid markers for age estimation of white abalone collected during more recent years within the Southern California Bight (SCB).

Materials and methods

Abalone shells

Five white abalone shells collected from the SCB were analysed for $\Delta^{14}\text{C}$ and estimates of age. Only shells with a known collection date or year and known collection location were used. Known location was important in order to avoid potential issues associated with regional differences in patterns of $\Delta^{14}\text{C}$ deposition (e.g. shells from Baja California). The shells also had to be in adequate condition, such that areas of the prismatic layer were intact along the growth axis of maximum shell length (Fig. 1). Selected sample locations in the shell were usually not free of biotic and abiotic loss of material and microscopic examination (Olympus dissecting microscope, Tokyo, Japan) was used to select unaffected shell portions. The apex, or earliest shell growth, has the thinnest prismatic layer and was often not intact; however, the nacreous shell was considered acceptable for this

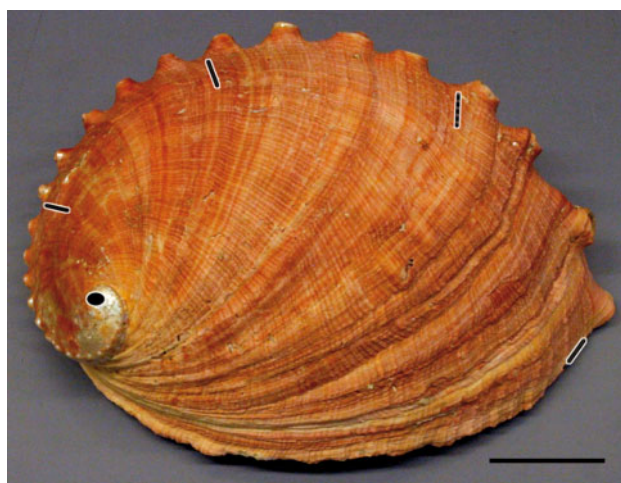


Fig. 1. Whole white abalone shell (1972-2), with sample locations denoted with outlined black bars. Locations sampled were the apex (0-mm MSL) and edge (193-mm MSL), with three intermediate samples at 50-mm, 100-mm and 150-mm MSL (scale bar = ~4 cm).

part of the shell when the apex included the earliest growth. As a verification of proper extraction of the earliest shell growth in the apex area, juvenile shell dimensions and shape were referenced. Most samples were located in museum archives with the best shells from the Santa Barbara Museum of Natural History ($n=4$) and one from a Proteus Farm aquaculture project (Table 1). Collection years ranged from 1967 to 1996, with shell sizes being from 151-mm to 200-mm MSL. All shells were collected from within the SCB, ranging from Santa Catalina Island to off Point Loma, San Diego, California.

Sampling design in this kind of study is usually focused on validating estimates of age from some form of growth-zone counting. White abalone has not been shown to have regular banding patterns that can be quantified (e.g. *Haliotis corrugata*, Shepherd and Avalos-Borja 1997); therefore, age was roughly calculated on the basis of the age and growth data from Tutschulte and Connell (1988). Sample locations across the shell were selected to date back through the informative period in bomb radiocarbon dating (between ~1955 and 1970). Edge material was taken from each specimen, except the most recently collected shell from Proteus Farm because its final few years of life were in aquaria, which was used to determine $\Delta^{14}\text{C}$ levels near the time of collection. The sampling series for each specimen proceeded from the edge sample through shell material that was accreted at younger ages (Fig. 1).

Shell-sample series

Each shell specimen was sampled in a manner that was suited for the collection year and a projection of the potential age back

through the period of rising marine $\Delta^{14}\text{C}$. WA 1967 was sampled on the edge and apex because of its proximity to the peak $\Delta^{14}\text{C}$ values anticipated for the year of collection. The three specimens collected in 1972 were sampled the most comprehensively because it was expected that the growth of each individual would either span the $\Delta^{14}\text{C}$ peak and rise, or some portion of it. WA 1996 was the only sample available that held promise of addressing the question of lifespan because it was collected nearly 30 years after the $\Delta^{14}\text{C}$ peak was reached for the $\Delta^{14}\text{C}$ rise (estimated as ~1967 to 1970 from other $\Delta^{14}\text{C}$ records). Therefore, two samples (each replicated) were taken at and near the apex to evaluate the $\Delta^{14}\text{C}$ values in the shell at the earliest age of the specimen.

Sample extractions were made at points along the growth axis (spiral) of the shell, following what would have been the MSL of the specimen (Fig. 1). A Dremel® rotary tool (Robert Bosch Tool Corporation, Mount Prospect, IL, USA) with a cutting wheel was used to cut small sections from the shell locations. Each was cut to a width of a few millimetres, with a length of up to 1 cm along the arc of the shell increments. The extracted portions included both prismatic and nacreous layers (Fig. 2), and the nacreous layer was mostly removed by grinding with a lapidary wheel. Each extracted portion provided variable amounts of prismatic material, the quality of which ranged from relatively pristine to highly eroded (endoliths (H. Hawk unpubl. data) and other forms of degradation). Each extracted portion of prismatic shell was treated with a series of cleaning procedures that ranged from sonication in ultra-pure water and weak acid (0.01 N HCl) to remove adhering material and degraded carbonate, to extensive

Table 1. Five white abalone shells (*Haliotis sorenseni*) were sampled in a time series for bomb radiocarbon dating

Individual sizes are maximum shell length (MSL). Sample MSL is the shell length of the individual when the sampled shell material was accreted (edge to apex to denote youngest to oldest). Radiocarbon values, reported as Fraction modern (Fm) and $\Delta^{14}\text{C}$, are adjusted for known or estimated formation year and corrected for $\delta^{13}\text{C}$ fractionation. Collection numbers are for Santa Barbara Museum of Natural History, except WA 1996 (Proteus Farm)

Shell ID (collection #)	Collection location and year	Water depth (m)	MSL (mm)	Sample MSL (mm)	Fraction modern	$\Delta^{14}\text{C}^{\text{A}}$ (‰)
WA 1967 (352560)	Santa Catalina December 1966	Unknown	151	151 (edge)	1.0612	59.0 ± 3.5
				0 (apex)	1.0542 ^D	42.0 ± 3.4
WA 1972-3 (352558) ^B	Point Loma, San Diego 1972	10–20	165	165 (edge)	0.9672	-42.0 ± 4.0
				0 (apex)	1.0166	6.6 ± 3.5
WA 1972-2 (352558) ^B	Point Loma, San Diego 1972	10–20	193	193 (edge)	0.9546	-54.2 ± 3.4
				150	1.0384	27.3 ± 3.7
				100	0.9347	-66.5 ± 3.5
				0 (apex)	0.9242	-75.8 ± 3.5
WA 1972-1 (352558) ^B	Uncertain ^B 1961 (est.)	Unknown	195	195 (edge)	0.9347	-85.5 ± 3.2
				169	0.9444	-56.9 ± 3.6
				140	0.9456 ^D	-61.0 ± 3.9
				109	0.9314	-75.5 ± 3.5
				83	0.9164	-90.9 ± 3.5
				0 (apex)	0.9315	-77.2 ± 3.5
WA 1996 (143)	Los Angeles ^C 1996 \pm 2 years ^C	Unknown	200	61	0.9259	-95.0 ± 3.5
				0 (apex)	1.0521	-83.5 ± 3.5
				1.0406 ^D	44.7 ± 3.7	
				0 (apex)	1.0792	38.1 ± 5.2
					1.0757 ^D	76.6 ± 3.5
						68.1 ± 3.0

^AAdjusted for fractionation with an assumed $\delta^{13}\text{C}$ value of 1, or close to 1 where $\delta^{13}\text{C}$ was measured (range -0.1 to 2.1 ‰).

^BAll shells were in the same collection box at SBMNH.

^CCollection location generally known with a year of death between 1994 and 1998 (Tom McCormick, Proteus Farm).

^DReplicate sample.

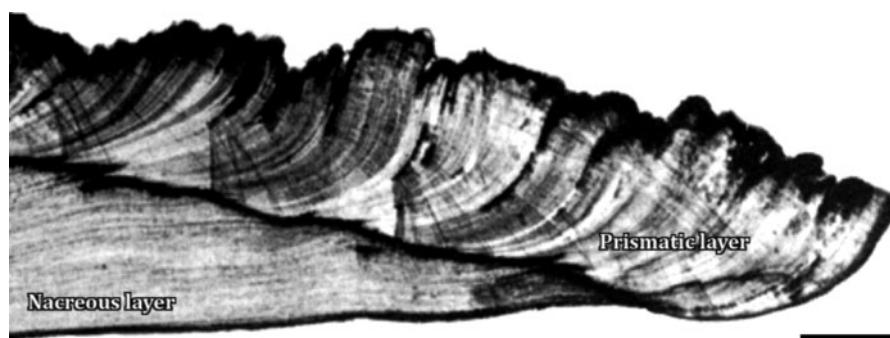


Fig. 2. Cross-section of an abalone shell showing how the shell material is structured (modified from Bevelander 1987). The outer prismatic layer was targeted for sampling because of its greater time-specificity, relative to the more splayed growth pattern of the nacreous layer. A small block was cut from the prismatic layer for sample processing (scale bar = ~1 mm).

microscopic examination with removal of endolithic material with a fine-tipped probe, followed by repeated sonication and weak acid treatments. Samples were considered finished when only small grains of clean abalone shell were visible under a dissecting microscope (ranging in weight from 5 to 27 mg).

These samples were submitted as carbonate to the Center for Accelerator Mass Spectrometry at Lawrence Livermore National Laboratories for radiocarbon measurement using standard preparation procedures for analysis on an accelerator mass spectrometer (AMS). Values for radiocarbon were reported as Fraction modern (Fm), which were converted to $\Delta^{14}\text{C}$ in reference to an established pre-nuclear-age radiocarbon record (Stuiver and Polach 1977) and standardised for isotopic fractionation. An assumed delta carbon-13 ($\delta^{13}\text{C}$) value of 1 was used to correct for fractionation (based on the mean measured value from other shells), except for samples where $\delta^{13}\text{C}$ was measured (-0.1 to 2.1%). In addition, dates of collection and near year-of-formation dates were used to adjust $\Delta^{14}\text{C}$ values for modern time (since 1950); pre-bomb required no adjustment from 1950, but an assumed year of 1960 was used for the rise $\Delta^{14}\text{C}$ values and 1970 was used for the near-peak $\Delta^{14}\text{C}$ values. These adjustments minimised potential differences for the comparison of these data with the reference $\Delta^{14}\text{C}$ data.

Regional $\Delta^{14}\text{C}$ reference

To provide a temporal calibration for the measured $\Delta^{14}\text{C}$ in white abalone shell samples, a series of records were compiled to describe the temporal nature of the regional $\Delta^{14}\text{C}$ signal (Fig. 3). The nearest complete $\Delta^{14}\text{C}$ records were from otoliths of yelloweye rockfish (*Sebastes ruberrimus*; Kerr *et al.* 2004; A. H. Andrews, unpubl. data) and Pacific halibut (*Hippoglossus stenolepis*; Piner and Wischniowski 2004). To provide a regional abalone context to the comparisons, a series of known-age abalone shell samples from within the SCB were analysed for $\Delta^{14}\text{C}$ (Table 2). The additional samples covered the periods of pre-bomb to post-bomb decline. In addition, measurements of dissolved inorganic carbon (DIC) from various locations and points in time were considered (Linick 1978; Robinson 1981; Druffel and Williams 1991; Williams *et al.* 1992). A local regression (Loess curve) was fit to the revised yelloweye rockfish $\Delta^{14}\text{C}$ data to provide a general indication of the central distribution of the time series, which was reinforced with the

known-age abalone samples and concurrent $\Delta^{14}\text{C}$ rise documented with Pacific halibut $\Delta^{14}\text{C}$ record. The measured $\Delta^{14}\text{C}$ values from some white abalone samples could be assigned to the period of rising $\Delta^{14}\text{C}$ (diagnostic values) and were given a year-of-formation based on this median Loess curve estimate. A range of possible years for the sample formation was estimated based on the 95% CI of the yelloweye rockfish $\Delta^{14}\text{C}$ data, a range taken into consideration when estimating age and growth.

Growth function

The information associated with each sample point consisted of the estimated year-of-formation, the $\Delta^{14}\text{C}$ value, and the MSL of the specimen where the sample was extracted. The distance of each sample location to the edge of the shell was used to determine the potential age range of the formation period. We used a two-parameter von Bertalanffy growth function (Fabens 1965),

$$L_t = L_\infty(1 - e^{-kt}),$$

to evaluate the range in ages when the sample was formed. To do this, we used an iterative procedure where the value of the mean asymptotic shell length was fixed $L_\infty = 210\text{-mm MSL}$, Tutschulte and Connell 1988). Iterations were performed by changing the value of the von Bertalanffy growth function parameter k to match the estimated year-of-formation and associated 95% CI determined from $\Delta^{14}\text{C}$ analysis. Additionally, we explored how the estimated age of the sample and k -values changed at $\pm 5.0\text{ mm}$ from the sample. Results from iterative fits of the von Bertalanffy growth function were reported as a value with a range that covered the potential variation in the year-of-formation, leading to a range in the k -values. Extrapolation of the fitted functions provided estimates of lifespan for some shells that extended into the pre-bomb period.

Results

Bomb radiocarbon values and dates

Measurements of $\Delta^{14}\text{C}$ from the white abalone shell-sample series ranged, as expected, from pre-bomb to post-bomb (Table 1). Determination of dates associated with the values was

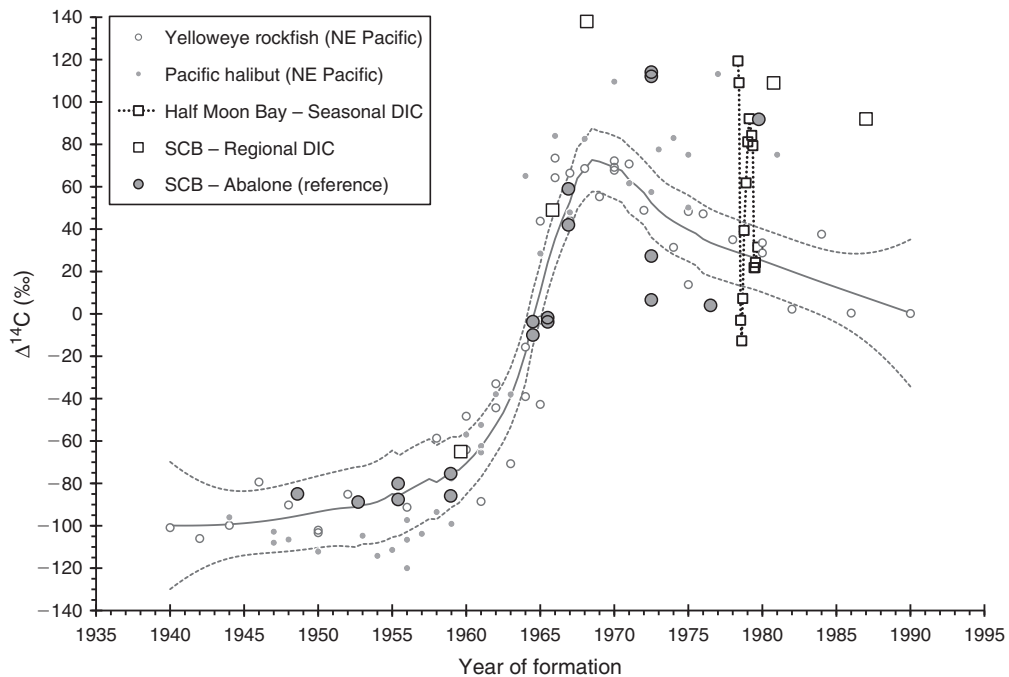


Fig. 3. Measured $\Delta^{14}\text{C}$ values from known-age white abalone shell material, plotted with a compilation of regional $\Delta^{14}\text{C}$ reference records from various sources along the coastal margin of the north-eastern Pacific Ocean. Results from abalone shell were similar in the timing of the rise and amplitude of $\Delta^{14}\text{C}$ when compared to the closest comprehensive $\Delta^{14}\text{C}$ records (derived from otoliths of two fishes in the Gulf of Alaska). In addition, a high degree of post-peak $\Delta^{14}\text{C}$ variability was documented from the shell material. Other $\Delta^{14}\text{C}$ records of interest were from within or near the Southern California Bight (SCB) as individual measurements of dissolved inorganic carbon (DIC) from seawater. The yelloweye rockfish data have been fitted with a Loess curve (spline interpolation smoothing parameter = 0.5, two-parameter polynomial; SigmaPlot 11.2), to provide a central distribution reference for the $\Delta^{14}\text{C}$ data series with a 95% CI.

a combination of known-age edge material and alignment to the reference series (Fig. 4). Lowest values were from two shells that were living during the pre-bomb period (WA 1972-1 and WA 1972-2), with values that were similar to the pre-bomb reference abalone $\Delta^{14}\text{C}$ data (mean \pm s.d. = $-83.7 \pm 5.0\%$; $n = 6$). The greatest $\Delta^{14}\text{C}$ values were from the most recently collected shell (WA 1996), with a mean of 72.3% , being equivalent to the peak values recorded for yelloweye rockfish, but less than the other references. Temporal correlation was somewhat arbitrary for this shell because of the regional variability in the $\Delta^{14}\text{C}$ signal and is considered an age estimate. The known-age $\Delta^{14}\text{C}$ values from the edge of shells provided reference points that supported projection of $\Delta^{14}\text{C}$ values to the period of the first rise in $\Delta^{14}\text{C}$ (Table 2). The $\Delta^{14}\text{C}$ values from two shells provided a good fit to the reference chronology (WA 1967, WA 1972-2), one being slightly lower than expected (WA 1972-3), and one indicating that the collection date was not accurate (WA 1972-1; Fig. 4). Edge material from shells WA 1967 and WA 1972-2 provided $\Delta^{14}\text{C}$ values similar to the reference chronology, with the highest confidence in terms of providing age and growth characteristics. The $\Delta^{14}\text{C}$ value from the edge of specimen WA 1972-1 could not be assigned a year of formation of 1972 because the $\Delta^{14}\text{C}$ value was too low ($-61.0 \pm 3.9\%$) relative to the reference curve and was assigned a year-of-formation of 1961 (based on the Loess curve). Further adjustment to the uncertainty of selecting 1961 (95% CI) was

not considered because the value of the sample series became useful only as pre-bomb reference material. Apex material from the 1996 shell provided $\Delta^{14}\text{C}$ values that could be attributed to a year-of-formation associated with near-peak $\Delta^{14}\text{C}$ values, but could have been younger based on the regional $\Delta^{14}\text{C}$ reference variation. In addition, greater uncertainty in the collection year (± 2 years) was revealed for WA 1996 after analyses had been performed. Each of the $\Delta^{14}\text{C}$ values fitted to the reference chronology using the Loess curve and each was given a range for the potential period of formation based on the 95% Loess CI, with the exception of WA 1972-1, as stated previously (Fig. 4).

Regional $\Delta^{14}\text{C}$ reference

Compilation of the regional $\Delta^{14}\text{C}$ reference from otoliths, DIC and known-age abalone shell material led to a pattern of rapid rise in $\Delta^{14}\text{C}$, with highly variable post-bomb amplitude (Fig. 3). Measured $\Delta^{14}\text{C}$ values from known-age shell material (collection years 1948–1979) ranged as suspected from fairly well constrained pre-bomb levels (mean \pm s.d. = $-83.7 \pm 5.0\%$) to elevated and variable post-bomb decline values (Table 2). Rise values were in close agreement with the otolith records in the early 1960s and provided support for the alignment of samples from other shells of unknown age. Peak and post-peak values were variable and differed on the order of 100% for similar dates. This difference was similar to what was documented by

Table 2. Southern California Bight $\Delta^{14}\text{C}$ reference series from abalone shells

Collection numbers are for Santa Barbara Museum of Natural History. Shell size is maximum shell length (MSL) and radiocarbon results are from edge material (prismatic layer) taken near MSL. Radiocarbon values, reported as Fraction modern (Fm) and $\Delta^{14}\text{C}$, are adjusted to collection date or year and corrected for $\delta^{13}\text{C}$ fractionation. Three shells in this set were sampled further for a $\Delta^{14}\text{C}$ time series used in bomb radiocarbon dating (Series). WA = white abalone (*Haliotis sorenseni*) and RA = red abalone (*H. rufescens*). n.m. = Not measured

Shell ID (collection #)	Collection location and date or year	Water depth	MSL (mm)	Fraction modern	$\Delta^{14}\text{C}$ (‰)
WA 1948 (116192)	Santa Barbara Island August 1948	5 fathoms (9 m)	184	0.9148	-85.0 ± 3.8
WA 1952 (122917)	San Clemente Island September 1952	70 feet (21 m)	102	0.9188	-88.4 ± 3.5
WA 1955 (129843)	San Clemente Island May 1955	Unknown	170	0.9130 0.9205 ^D	-87.6 ± 2.9 -80.1 ± 3.1
RA 1958 ^A (130608)	Santa Cruz Island 2 December 1958	Unknown	211	0.9255 0.9150 ^D	-75.4 ± 3.2 -85.9 ± 3.1
WA 1964 (349096)	Channel Islands 1964	Unknown	148	0.9880 0.9917 ^D	-3.7 ± 3.4 -10.0 ± 3.2
WA 1965 (352559)	Santa Rosa Island 1965	Unknown	154	1.0000 0.9980 ^D	-1.8 ± 3.7 -3.8 ± 3.2
WA 1966 (Series) (352560)	Santa Catalina Island December 1966	Unknown	151	1.0612 1.0542 ^D	59.0 ± 3.5 42.0 ± 3.4
WA 1972-2 (Series) (352558) ^B	Point Loma, San Diego 1972	10–20 m	193	1.0384	27.3 ± 3.7
WA 1972-3 (Series) (352558) ^B	Point Loma, San Diego 1972	10–20 m	165	1.0166	6.6 ± 3.5
WA 1972-4 (352558) ^B	Point Loma, San Diego 1972	10–20 m	135	1.1163 1.1164 ^D	$113.0 \pm 3.4^{\text{C}}$ $113.0 \pm 3.8^{\text{C}}$
RA 1976 (352503)	Point Conception 31 December 1976	Unknown	n.m.	1.0072	4.0 ± 3.4
RA 1979 (2397)	Oil Platform off Gaviota 3 October 1979	55 feet (17 m)	n.m.	1.0957	91.8 ± 4.3

^ANoted as 'presumed hybrid.'

^BAll shells under the same museum accession number.

^CPlotted as 112.0‰ and 114.0‰ to provide visible separation of the two measurements in figures.

^DReplicate sample.

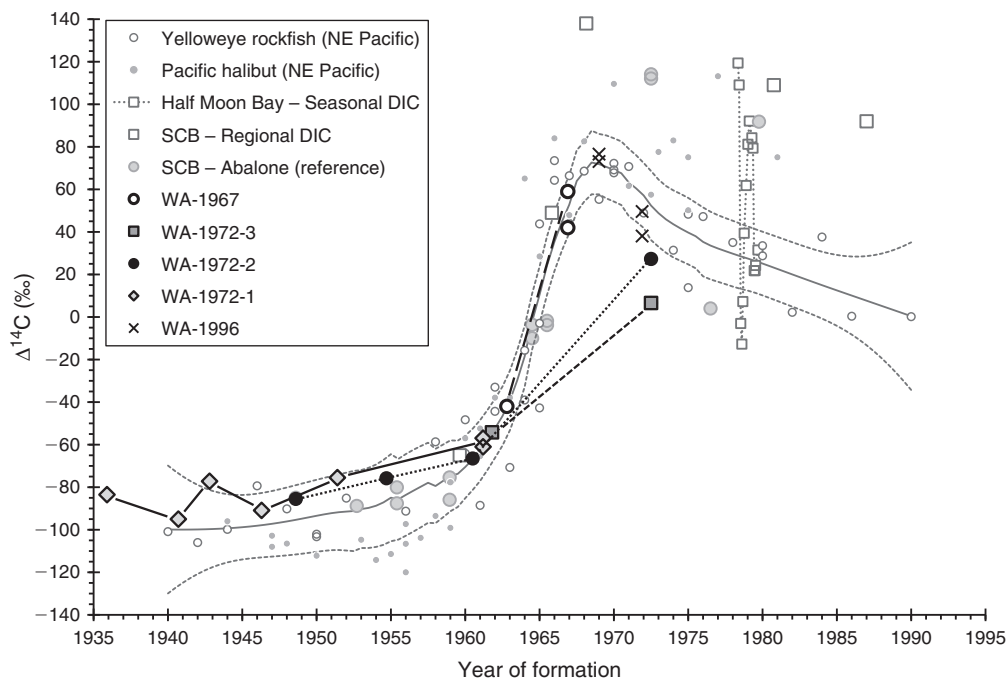


Fig. 4. Bomb radiocarbon plot of results from large white abalone shells, with compiled $\Delta^{14}\text{C}$ reference data from various sources (see Fig. 3). White abalone $\Delta^{14}\text{C}$ data were plotted based on collection-year data and diagnostic $\Delta^{14}\text{C}$ values were fitted to the rise in $\Delta^{14}\text{C}$. Beyond these values (pre-1958), the measured $\Delta^{14}\text{C}$ values from other parts of the shell were plotted in time using the calculated von Bertalanffy growth functions (VBGF) for each shell (Table 2).

Robinson (1981), which is the only continuous DIC record that provides a measure of annual variation as a result of seasonal changes (Fig. 3).

Growth estimates

Von Bertalanffy growth functions fitted to the period of shell formation and the change in shell length provided a range of growth scenarios for each shell (Table 3). Because there was a potential range in the year-of-formation for what was considered the diagnostic $\Delta^{14}\text{C}$ values, the result was a predicted k -value or growth-constant range for each shell. Growth constants provided an indication that shell growth was highly variable, with a range of $0.105\text{--}0.305\text{ year}^{-1}$ (uncertainty of $0.074\text{--}0.368\text{ year}^{-1}$). The smallest and youngest animal (WA 1967) shell grew most rapidly and the slowest-growing were the two largest shells (WA 1972-2 and 1996). An investigation of the effect of changing L_∞ from 200-mm MSL by ± 5 mm on k -values for each shell revealed only minor differences in k -values. These minor differences are not reported because of greater uncertainty associated with the year-of-formation chosen from the Loess 95% CI.

Age estimates

From the $\Delta^{14}\text{C}$ data and the estimated growth parameters, age was estimated for all of the shells with post-bomb collection years (Table 4). Age was extrapolated for the other two shells (WA 1972-1 and 1972-2) based on information from other shells or the range in fitted k -values. For specimen WA 1972-1, the collection year was not in agreement with the year applicable for the measured $\Delta^{14}\text{C}$ at the shell edge (assigned a birth year of 1961); hence, an assumption was made that the shell had a growth trajectory similar to that of WA 1972-2 (shell size and structure were similar and the shells were collected from the same location), resulting in a calculated age of ~ 25 years. The utility of this projection is strictly for establishing a pre-bomb record for white abalone from the region, and the age estimate is not considered critical for this reason. For WA 1972-2, a projection from the known period of formation (outer 43 mm of shell in ~ 12 years) to the MSL led to an estimated age at collection of 24 years. Each of these age determinations has a relatively high margin of uncertainty; however, this is likely to be a conservative margin. More precise ages were determined

Table 3. Diagnostic portions of shell growth providing measures of age and growth

Formation time was calculated based on the difference between the known collection date and a temporal reference point in the $\Delta^{14}\text{C}$ reference series that corresponded to the measured $\Delta^{14}\text{C}$ level (centred on the Loess curve). The first value for each is the collection year and second was determined from the fit to the Loess curve. The uncertainty of the $\Delta^{14}\text{C}$ reference dates is reflected in the calculated formation time as a range in parentheses. For k , L_∞ was chosen as 210-mm MSL from Tutschulte and Connell (1988)

Shell ID	$\Delta^{14}\text{C}$ (‰)	Year of formation ^A	Formation time (years)	Length change (mm)	k (year^{-1}) (range) ^B
WA 1967	59.0 ± 3.5	1966.9	4.1	151	0.305
	42.0 ± 3.4		(3.4–5.4)	(0–151)	(0.230–0.368)
	-42.0 ± 4.0	1962.8 (+0.8/–1.3 years)			
WA 1972-2	27.3 ± 3.7	1972.5	12.0	43	0.105
	-66.5 ± 3.5	1960.5	(11.9–23.9)	(150–193)	(0.074–0.120)
		(+1.5/–5.0 years)			
WA 1972-3	6.6 ± 3.5	1972.5	10.7	165	0.144
	-54.2 ± 3.4	1961.8	(9.5–12.5)	(0–165)	(0.123–0.162)
		(+1.2/–1.8 years)			
WA 1996	n.m.	1996 ± 2 years	27.0	200	0.113
	76.6 ± 3.5	1969.0	(22.0–30.5)	(0–200)	(0.100–0.139)
	44.7 ± 3.7	(+3.0/–1.7)			

^AYear of formation determined from either year of collection or based on a diagnostic fit of a given rise or peak $\Delta^{14}\text{C}$ value to the Loess reference curve.

^B L_∞ was chosen as 210 mm MSL from Tutschulte and Connell (1988).

Table 4. Summary of estimated age data for the white abalone shells used in the study

Because collection year and shell size varied considerably, each shell had unique circumstances in making the age estimations. Specifically, 1972-1 was extrapolated, after reclassifying with a collection year of 1961, to provide a pre-bomb $\Delta^{14}\text{C}$ reference series that was in agreement with other shell material of known age

Shell ID	Year of collection	Birth year	MSL (mm)	Shell age
WA 1967	1966.9	1962.8 (1961.5–1963.6)	151	4.1 (3.4–5.4)
WA 1972-1	1961 ^A	1935.9 (1925.3–1939.0) ^A	195	25.1 (22.0–35.7) ^A
WA 1972-2	1972.5	1948.6 (1938.5–1951.6) ^B	193	23.9 (20.9–34.0) ^B
WA 1972-3	1972.5	1961.8 (1960.0–1963.0)	165	10.7 (9.5–12.5)
WA 1996	1996	1969.0 (1967.4–1972.0)	200	27.0 (22.0–30.5)

^ASelected median year from Loess curve fit and extrapolated age assuming growth characteristics similar to those of 1972-2.

^BExtrapolated age and growth, based on diagnostic fit to the rise of $\Delta^{14}\text{C}$ value at 150 mm.

for shells with $\Delta^{14}\text{C}$ values in the diagnostic portion of the reference curve and measured from the apex of the shell, encompassing the full lifespan. The estimated age of these shells was 4, 11 and 27 years old for shell lengths of 151-mm, 165-mm and 200-mm MSL (WA 1967, 1972-3 and 1996), respectively. Given these estimates, lifespan of white abalone can approach 30 years.

Discussion

Age and growth estimates

Bomb radiocarbon dating has provided estimates of age for a collection of white abalone shells and the results are consistent with those of earlier studies. Previous studies have indicated that early growth is well documented up to 10 years of age and an extrapolation of those data to the maximum size (210-mm MSL) provided a lifespan estimate of ~35 years (Tutschulte and Connell 1988). The largest shell in the present study was 10 mm smaller than the estimated maximum size for white abalone. This implies that lifespan could be greater than 30 years, as was predicted from the present work, and that a maximum lifespan of 35 years is reasonable.

Abalone are known to exhibit individual variation in growth (Sainsbury 1980), which can affect both k (some individuals growing slower or faster) and L_∞ (allowing for differences in the mean final size for the population). A greater estimate of lifespan is supported when alternative growth scenarios are considered. For example, the largest specimen we examined had an estimated $k = 0.100\text{--}0.139\text{ year}^{-1}$ and could be 27–32 years old at 97% of the maximum asymptotic length ($L_\infty = 210\text{-mm MSL}$). If L_∞ is increased by 5 mm in MSL, the time required to reach 97% of maximum size could be up to 37 years. Given that the von Bertalanffy growth function and other measures of growth tend to overestimate early growth rates (Yamaguchi 1975, Rogers-Bennett *et al.* 2007), it is suggested that lifespan is close to 30 years. Another consideration is that shell loss has been documented in tag-recapture studies of other species of abalone, with the inclusion of negative growth data resulting in an increase in the von Bertalanffy k -value (Button and Rogers-Bennett 2011). However, this would affect only estimates of projected age and would lead to an underestimate of the maximum age; shell loss would not change age estimates from measured $\Delta^{14}\text{C}$ values.

The age determinations from the smaller shells in the present study can be further evaluated based on observations of growth, flexibility in the iterative fit of the von Bertalanffy growth functions, and potential variations in regional $\Delta^{14}\text{C}$ records. The WA 1967 shell was perhaps the most informative in terms of indicating a maximum growth-rate potential for white abalone. The lower limit for growth is well defined by the rise in $\Delta^{14}\text{C}$ at $k = 0.230\text{ year}^{-1}$. On the other extreme, it is likely that the youngest age estimate for this shell (3.4 years) is not possible because growth would have had to occur much faster than what has been observed in other empirical studies (Tutschulte and Connell 1988); hence, the growth trajectory for this 151-mm-MSL shell can be more realistically described as $k = 0.230\text{--}0.305\text{ year}^{-1}$ and age of ~4–5 years. Similar scenarios can be applied to the other shells where iterative fits of von Bertalanffy

growth functions are applied to a conservative year-of-formation uncertainty (95% CI). However, this kind of speculation highlights the need for a better regional $\Delta^{14}\text{C}$ record. At this time, the $\Delta^{14}\text{C}$ time series from yelloweye rockfish and Pacific halibut from the Gulf of Alaska provides the closest references to use for calibration purposes. Although it is desirable to define the characteristics of the $\Delta^{14}\text{C}$ changes in the SCB, it is likely that the rise period is similar for coastal areas of the north-eastern Pacific Ocean. In support of this argument is the magnitude and timing of the measured $\Delta^{14}\text{C}$ values from edge material from the WA 1967 specimen, as well as the other reference abalone $\Delta^{14}\text{C}$ data. Although it is clear that post-bomb $\Delta^{14}\text{C}$ variation is great for the region, it is likely that the $\Delta^{14}\text{C}$ rise in the early to mid-1960s was well constrained.

Bomb radiocarbon values and regional references

Pre-bomb values can be used to establish a $\Delta^{14}\text{C}$ threshold to understand what $\Delta^{14}\text{C}$ values represent the initial $\Delta^{14}\text{C}$ rise in the SCB. The shell that was determined to have a 1961 birth year provided a long time series of pre-bomb values for the region. Given the calculated growth trajectory for this shell, the record of pre-bomb $\Delta^{14}\text{C}$ values was estimated to extend back 22–36 years from 1961. Despite the shell-age uncertainty and the year of formation of the extracted material, it is certain that this series of samples is representative of $\Delta^{14}\text{C}$ levels before significant atmospheric testing. The mean pre-bomb $\Delta^{14}\text{C}$ value for this series ($-84.4 \pm 8.5\text{‰}$, s.d.) was consistent with the regional pre-bomb shell reference values ($-83.7 \pm 5.0\text{‰}$), and greater than pre-bomb $\Delta^{14}\text{C}$ levels in the Gulf of Alaska (Kerr *et al.* 2005). The elevated trend in pre-bomb $\Delta^{14}\text{C}$ for the SCB is intermediate to subtropical pre-bomb levels of the northern Pacific (Druffel 1987), and most similar to regions affected by strong upwelling (i.e. Galapagos, Druffel 1981). Given a combined record of all pre-bomb abalone shell data (mean = -83.5‰ , $n = 13$), the year-of-formation for shell material with a $\Delta^{14}\text{C}$ value slightly exceeding 2 s.d. of this mean ($> -70.9\text{‰}$) can be classified as the first rise of $\Delta^{14}\text{C}$ (Kerr *et al.* 2005). This observation and the temporal alignment are further supported by the known-age shell samples that are consistent with the $\Delta^{14}\text{C}$ rise in the mid- to late 1960s.

This analysis of radiocarbon in white abalone shell material is subject to multiple sources of imprecision. The first is the highly variable nature of $\Delta^{14}\text{C}$ measured in the post-bomb abalone shell material, consistent with the dynamic marine environment of the SCB. The coastal regions of the north-eastern Pacific Ocean are prone to strong and variable upwelling, leading to complex seasonal and annual cycles that ebb and flow with deep-water sources depleted in ^{14}C (Robinson 1981; Rau *et al.* 2001; Haltuch *et al.* 2013). Despite the seasonal variability, the temporal specificity of the $\Delta^{14}\text{C}$ rise is evident among records, and was supported by known-age shell material. The first rise $\Delta^{14}\text{C}$ values, once defined relative to regional pre-bomb levels, remain diagnostic and are most informative for assigning a year-of-formation with some level of quantitative uncertainty (95% CI), as was the case in the present study. The second source of imprecision in our analysis is the use of the two-parameter von Bertalanffy growth function to model growth of the white abalone. A variety of alternative growth

models have been devised and evaluated to model individual growth, and these models vary in the number of parameters that are estimated and their assumptions about individual growth dynamics. Rogers-Bennett *et al.* (2007) analysed the relative quality of a suite of growth models to describe mean length-at-age and found that the three-parameter logistic and Richards' functions provided a comparable and superior fit to the von Bertalanffy growth function to describe red abalone length-at-age. Because of our desire to perform the iterative fitting procedure by altering a single model parameter, and fixing the value of L_{∞} , and its computational simplicity, we performed the analysis using the two-parameter variant of the von Bertalanffy growth function. The use of such a parsimonious model is justified, given the limited data available for the endangered white abalone.

The present work represents an expansion of radiocarbon ageing methods to the SCB and it is therefore desirable to understand how bomb radiocarbon has entered this environment. Records from Baja California and the north-eastern Pacific aid in our understanding of the potential variability, but also the temporal specificity of the $\Delta^{14}\text{C}$ rise and decline over time (e.g. Frantz *et al.* 2000; Ebert and Southon 2003; Piner *et al.* 2005; Andrews *et al.* 2007; Haltuch *et al.* 2013). The determination of age for the 1996 white abalone shell was based on a fit to peak $\Delta^{14}\text{C}$ values from the yelloweye rockfish record, with a notable drop in $\Delta^{14}\text{C}$ levels for the more recent shell growth. Within 61-mm MSL, or >3 years according to Tutschulte and Connell (1988), the change in $\Delta^{14}\text{C}$ was a decrease of 20–30%. Other records from the northeastern Pacific are not as well defined in terms of peak $\Delta^{14}\text{C}$ values and timing. Some provide records that do not decline substantially post-bomb, making age determinations for near-peak $\Delta^{14}\text{C}$ values dubious, imprecise or impossible (e.g. see post-bomb records in Frantz *et al.* (2000) and Piner *et al.* (2005)). The $\Delta^{14}\text{C}$ signal in the SCB appears to follow a rapid rise that is similar in timing to other records, but is followed by a complicated post-bomb decline that is punctuated with strong inter-annual and seasonal oscillations.

Implications of white abalone age

Bomb radiocarbon dating of white abalone shells has provided estimates of age, growth and lifespan from large adult shells and can be related to previous work. The use of empirical evidence provided sound age estimates, with a marginal level of uncertainty where no age was previously determined. Growth was variable among shells, with potential k -values ranging from ~ 0.105 to 0.305 . The lifespan of animals 151-mm to 200-mm MSL was ~ 4 –27 years old. Lifespan estimates of nearly 30 years made in previous studies are consistent with the findings of the present study. These independent estimates of age provide a basis for greater confidence in the execution of proposed measures in the ESA white abalone recovery plan (National Marine Fisheries Service 2008).

The goal of the ESA recovery plan is to increase the abundance of white abalone to viable and self-sustaining levels. The results of the present study will help in achieving the goal of increasing the abundance of white abalone by providing information for the following two recovery actions: (1) developing and refining population data and demographic

population-viability models that will be used to evaluate threats, population trends and make predictions about future trends following restoration activities; and (2) guiding the protocols for brood-stock collection as a part of a captive propagation and enhancement program. In the first instance, the age, growth and lifespan estimates generated in the present study can be incorporated into predictive models that will help identify factors that have the greatest effect on population growth following restoration activities, such as aggregation or enhancement using captive-reared animals. Trustworthy estimates of lifespan, combined with an understanding of the reproductive potential of individuals over the lifespan, are needed to choose an enhancement strategy that will maximise population growth until self-sustaining densities are attained. Future studies should focus on understanding what factors control the reproductive potential of white abalone. In the second instance, the estimated maximum shell length, corresponding age estimation and lifespan estimate may guide the process for selecting which individuals are the best candidates for brood-stock collection. Animals that are large (>190 -mm MSL) and solitary are likely to be approaching their maximum age and may have very low reproductive potential; thus, these individuals could be good candidates. Given that recent surveys have suggested that the wild white abalone population is composed primarily of large (>100 -mm) individuals (Butler *et al.* 2006; Stierhoff *et al.* 2012), the age data presented here provide an indication that natural mortality is likely to occur for these animals in less than 20 years. This highlights the critical and timely need for restoration and implementation of the white abalone recovery plan.

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