Age-validated Longevity of Fishes: Its Importance for Sustainable Fisheries

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Marine fisheries have spread to the deep-sea because the fishes in many of the shallow-water marine habitats have been overexploited. Many studies have found that deep-sea fishes generally grow slowly and can achieve long life spans; however, most age estimates have not been validated. Several methods for validating age and growth estimates have been developed and applied to deep-water and other long-lived organisms. These include lead-radium and bomb radiocarbon dating of calcified structures. Application of these techniques has usually validated high lifespan estimates, some in excess of a century. In this paper, we discuss the applications and limitations of these techniques for difficult-to-age fishes. Because many fishery management techniques focus on biomass or yield and not as much on life history stages of fished populations, we specifically focus on the relevance of age validation to fishery management of deep-dwelling fishes, especially relative to slow growth, late age at maturity, long life spans, and the relative contribution of big, old, fecund females (BOFFs) and maternal-age-dependent larval survival to future generations via lifetime fecundity. These life history traits make their populations more vulnerable to fishing mortality, thus emphasizing the need to accurately assess longevity in fishes.

KEYWORDS age validation; bomb radiocarbon; carbon-14 (Δ^{14}C); deep-water fishes; fecundity; fishery management; growth; life history; life span; lead-radium dating; longevity; maternal-age-dependent larval survival; mortality; vulnerability

1. Introduction

Many marine fisheries are reported as overexploited on a global scale (Pauly *et al*. 2003). This overexploitation appears to have influenced the relative abundance of predatory fishes in some marine ecosystems (Pauly 1995; Worm *et al*. 2005) and may have upset the balance of some major ecosystems (Pauly and Christensen 1995; Pauly *et al*. 1998, 2002, 2003; Christensen *et al*. 2003; Frank *et al*. 2005). There is argument about the extent and the causes of these fishery declines and ecological impacts (Pauly 1995; Pauly *et al*. 1998, 2002, 2003; Myers *et al*. 2003; Myers and Worm 2003, 2005; Walters 2003; Hutchings and Reynolds 2004; Safina *et al*. 2005; Sibert *et al*. 2006; Worm *et al*. 2005; Hilborn 2007). However, it is certain that many near-shore fisheries have been so highly overexploited that fishing effort has moved further offshore and into deeper water (Clark 2001; Gordon 2001; Haedrich *et al*. 2001; Roberts 2002; Stockley *et al*. 2005).

Fishery modeling and management practices have primarily focused on stock assessments, which mainly use biomass and maximum (MSY) or optimum (OSY) sustainable yield, to attempt to determine the level of exploitation or sustainability of a given fishery (Hilborn and Walters 1992; Gallucci *et al*. 1996; Berkeley 2006). In some cases, numerical abundance and/or age composition were taken into consideration, but even age-structured analyses often make major assumptions about age-driven biological quantities. Because the complexities of population age-structure are poorly understood, dynamic parameters that are an important consideration must be modeled or assumed to be fixed (e.g., Methot 1990; Millar and Methot 2002). Stock assessments are now commonly performed, but the concept of sustainability is still very much in question (Millar and Methot 2002; Methot and Piner 2002; Ralston *et al*. 2003; Beamish *et al*. 2006; Longhurst 2006).

Fishing practices in many cases have caused the size (and presumably age) structure of many populations to be fished down (Mason 1998; Pauly *et al*. 1998; Worm *et al*. 2005; Harvey *et al*. 2006), and this may have seriously impacted long-lived fishes like chondrichthyans and those in the deep sea. In nearshore environments along the west coast of the U.S. there is evidence of significant shifts downward in the size composition of rockfish landings (Mason 1998). This fished-down size and age structure can have numerous impacts and a few of the most significant are further discussed here.

First, it can cause a loss of genetic diversity or heterozygosity (e.g., Hauser *et al*. 2002). In addition, some fishes are genetically structured at the regional and sub-regional scales, as was demonstrated for Patagonian toothfish (*Dissostichus eleginoides*; Rogers *et al*. 2006) and further described in otolith elemental analyses (Ashford *et al*. 2007), which influences how fishing might affect the genetic structure of populations. Stockley *et al*. (2005) demonstrated that the deep-sea black-spot sea bream (*Pagellus bogaraveo*), which was heavily fished in recent years due to depletion of shallow-water fish stocks, may have undergone a severe bottleneck in its genetic population structure; low genetic variability in its populations was documented due to the small population size that resulted from fishing.

Second, removing the larger individuals can favor slower-growing and earlier-maturing fishes (Kenchington 2002; Ziegler *et al*. 2007). Thus heritable differences in yield and life-history traits can be caused by selective fishing which has been demonstrated for fishes such as the northern cod (*Gadus morhua*; Novikov *et al*. 2002; Hutchings 2004; Olsen *et al*. 2004).

Third, there can also be long term ecological and evolutionary implications of size-specific fishing mortality, resulting in a "dynamic tug-of-war between natural and harvest selection" (Edeline *et al*. 2007) in

terms of size and age at first reproduction and size- and age-specific reproductive output (Conover and Munch 2002; Berkeley *et al*. 2004a; Bobko and Berkeley 2004; Berkeley 2006; de Roos *et al*. 2006; Walsh *et al*. 2006; Conover 2007; Jorgensen *et al*. 2007).

Fourth, there can be ecosystem effects (Frank *et al*. 2005; Scheffer *et al*. 2005; Worm *et al*. 2005) that can be manifested as loss of top carnivores and changes in trophic relationships of ecosystems. One management technique that can help alleviate this problem, at least on a local scale, is the implementation of Marine Protected Areas (MPAs; National Research Council 2001). These are being seriously considered and implemented in several places around the world, especially along the west coast of the United States (Parker *et al*. 2000). Berkeley (2006), however, pointed out that MPAs do not seriously consider the life histories of fished populations, except as sources of larvae for export from mature females.

Fifth, size-selective fishing has been estimated to cause a subsequent reduction in lifetime production, measured by O'Farrell and Botsford (2005, 2006a, b) as lifetime egg production (LEP) in rockfishes (Genus *Sebastes*; Family Scorpaenidae) and by Harvey (2005) as age-specific egg production. In addition, it can reduce survivorship of larvae from "fit" or well-adapted adults. It has been shown for some species that the larvae from these older females in some rockfishes are more numerous and robust, being stronger and more likely to survive (Love *et al*. 2002; Berkeley *et al*. 2004a, b; Bobko and Berkeley 2004; Berkeley 2006). And those larger, most likely older, females not only are often more fecund but they can also exhibit maternal-age-dependent increased larval survival. This has caused some authors to contend that fisheries, in general, need to "leave the big ones" (Birkeland and Dayton 2005).

2. The Importance of Age Validation in Estimating Longevity (Lifespan)

We propose here that the life history parameters longevity (length of life) and/or lifespan (average time between birth and death) are very important to consider when determining how to manage exploited populations. Long-lived fishes have often had their ages and life spans underestimated, causing fishery management policies to be less effective. This is not a new concept because the importance of age validation was strongly emphasized more than two decades ago by Beamish and MacFarlane (1983) and more recently by Campana (2001), among many other authors. However, many age, growth and longevity studies have not provided validated age estimates leading to the parameters determined in their studies.

Traditional age validation methods (mark-and recapture, laboratory rearing, or marginal increment analysis) are often difficult or impractical to use for long-lived or deep-sea fishes (Campana 2001). There was little hope for such applications to deepwater fishes until recent developments provided some promise for tagging deep-sea species *in situ*. This was pioneered by Starr *et al*. (2002) for eastern Pacific deep-water rockfishes, and used in other deep-sea applications (e.g. Sigurdsson *et al*. 2006) in deep water (~500–800 m) off Iceland on redfish (*Sebastes mentella*).

In lieu of such applications, a naturally occurring radioisotope pair found in calcified structures of fishes, radium-226 (^{226}Ra) and its daughter product lead-210 (^{210}Pb), can act as a built-in chronometer. In addition to this radiometric technique, atmospheric testing of thermonuclear devices in the 1950s and 1960s caused a rise in radiocarbon (Δ^{14}C) and produced a globally distributed signal that diffused into the ocean surface worldwide (Broeker and Peng 1982).

In recent years, many of the age estimates for deep sea fishes have been reevaluated and

in many cases were deemed drastically greater than previously suspected. A number of these age estimates, ones that were often met with disbelief because of the great longevity estimates, have been validated through use of lead-radium and bomb radiocarbon dating, some of which also included tag-recapture and oxytetracycline from field studies (e.g., Beamish and McFarlane 1983; Kastelle *et al*. 1994). Application of these radiometric methods has been successful for deep-sea fishes (e.g. Andrews *et al*. 1999, 2007) and this is especially true for a numerous rockfishes (Andrews *et al*. 2002, 2005, 2007; Bennett *et al*. 1982; Campana *et al*. 1990; Kastelle *et al*. 2000; Kastelle and Kimura 2006; Kerr *et al*. 2004, 2005; Piner *et al*. 2005; Stevens *et al*. 2004; Stransky *et al*. 2005; Watters *et al*. 2006). In some cases, complications in what appears to be a system that was not conserved with time provided circumstances that violated the necessary assumptions for successful application (e.g., cartilage of chondrichthyans and sturgeon; Burton *et al*. 1999; Welden *et al*. 1987). For otolith material, however, numerous other bony fishes have been validated using lead-radium and bomb radiocarbon dating (e.g., Fenton *et al*. 1991; Smith *et al*. 1991, 1995; Campana 1997; Andrews *et al*. 2001; Kalish *et al*. 2001; Ewing *et al*. 2007).

In this paper, we return to Beamish and McFarlane's (1983) plea for age validation to become a more common element in fish age and growth studies. In doing so, we will demonstrate the importance of age-validated longevity to fish population dynamics, especially in exploited conditions. We will also incorporate the results and concepts initiated by Berkeley *et al*. (2004a, b), Bobko and Berkeley (2004), and Berkeley (2006), in which they demonstrated the importance of larger, fecund female rockfishes (recently coined as "Big Old Fecund Females" or BOFFs), using the black rockfish (*Sebastes melanops*) aged 50 years old by counting rings in sectioned otoliths.

O'Farrell and Botsford (2005, 2006a, b) used size structure of the same species (*S. melanops*), but also included five other rockfish species to demonstrate the effect of size-selective fishing on LEP. They assumed that size classes represented age classes, but no age validation has been accomplished for these species. Similar studies have been done on rockfishes by Harvey (2005) and Harvey *et al*. (2006), assuming specific growth characteristics, not all of which were validated. Thus, it is important to note that the ages estimated or inferred from size-composition or otolith readings could leave some doubt about the reality of the BOFF and/or maternal-age-dependent larval survival, and perhaps the reduction in LEP. Hence, we emphasize use of age-validated species and that this perspective on age validation becomes more important when taking the previously stated factors into consideration.

3. The Importance of Lifetime Fecundity (Reproductive Output)

It is important to note that true reproductive output is a factor that can only be obtained by validating longevity or lifetime of a given species (Harvey 2005; O'Farrell and Botsford 2006a, b). In this paper, two terms will be used with regard to reproduction; fertility, the actual reproductive productivity or production of offspring, and fecundity, the physiological potential for reproduction or the age-specific state of being fertile. It appears that most fishes, including rockfishes, continue to reproduce after maturity, without evidence of senescence in all years following the age at first maturity (Cailliet *et al*. 2001). Because larger, and presumably older, fish often have higher fecundity and may have better adapted larvae, their lifetime fecundity becomes an important parameter in understanding and predicting population dynamics (Phillips 1964; Gunderson *et al*. 1980; Haldorson and Love 1991; Lea *et al*. 1999; Love *et al*. 1990, 2002; Berkeley

et al. 2004a, b; Bobko and Berkeley 2004; Harvey 2005; Berkeley 2006).

Summarized data on size-specific fecundity for rockfishes demonstrated that larger rockfishes typically produce more offspring (Love *et al.* 1990, 2002). Thus, fishing these larger size and older age classes heavily can truncate the number of reproductive years and thus reduce their ability to maintain viable populations. This has been demonstrated demographically by Ralston *et al.* (2003) for the shortbelly rockfish (*Sebastes jordani*) and by Ziegler *et al.* (2007) on the banded morwong (*Cheilodactylus spectabilis*). Also, environmental processes, like El Niño events, can also have a serious influence on reproductive output like egg production in fishes (Ven Tresca *et al.* 1995; Harvey 2005). We propose that this approach, using age-validated lifetime fecundity, should be a major research objective for all exploited fishes, including rockfishes.

Demographic approaches using either life table analyses or stage- and/or age-based matrices are good ways to produce predicted population dynamics, with and without exploitation (Cailliet 1992; Ebert 1999; Caswell 2001; Mollet and Cailliet 2002, 2003). In addition, sensitivity and elasticity analyses (Heppell *et al.* 2000; Frisk *et al.* 2005; Garcia *et al.* 2008) will allow the most ecological important life stages to be identified and used in fishery management policy. However, it may be that sustainability is unachievable (Longhurst 2002; 2006), especially without knowing these age-specific life history traits.

4. Deep-water Rockfish Age Determination, Validation, and Longevity

For this paper, we have chosen a few examples of age validation research on rockfish populations with which we are familiar off the west coast of the United States (Andrews *et al.* 2002, 2005, 2007; Kerr *et al.* 2004; Piner *et al.* 2005). We will focus on three species of rockfishes for which age has been validated, and life spans determined based on the maximum growth zone counts, for which one or both of the radiometric techniques (lead-radium or bomb radiocarbon dating) was used to support estimates of age.

Our bomb radiocarbon age-validation results on bocaccio (Andrews *et al.* 2005; *Sebastes paucispinis*) are useful relative to the papers cited above on black rockfish (*S. melanops*) because they are similar in terms of lifespan (~50 years), but perhaps not with regard to the other parameters as studied by Berkeley *et al.* (2004a, b) and Bobko and Berkeley (2004). We investigate both their size and age at maturity and their fecundity in this regard. We also present age-validated results for two other species on which we have published age-validation papers, the canary (*Sebastes pinniger*) and yelloweye (*Sebastes ruberrimus*) rockfishes, both of which have had their ages (and life spans) validated using lead-radium and bomb radiocarbon dating (Andrews *et al.* 2002, 2007; Kerr *et al.* 2004; Piner *et al.* 2005).

For these and other age estimation and validation studies, calcified structures such as otoliths, vertebrae, other bones, spines, and thorns have often proved useful and accurate. These structures are prepared for age determination in ways that enhance the readability of growth zones that are typically present. In age validation studies the use of core or growth zone specific material from adult structures and from various year classes have provided better age resolution than previously possible for both lead-radium and bomb radiocarbon dating.

Successful application of lead-radium and bomb radiocarbon dating to rockfishes (family Scorpaenidae) has a well developed history. The first application of lead-radium dating to otoliths in general was an age validation study on splitnose rockfish (*S. diploproa*) in which a 60 yr lifespan was supported from the growth-zone derived age estimation criteria (Bennett *et al.* 1982).
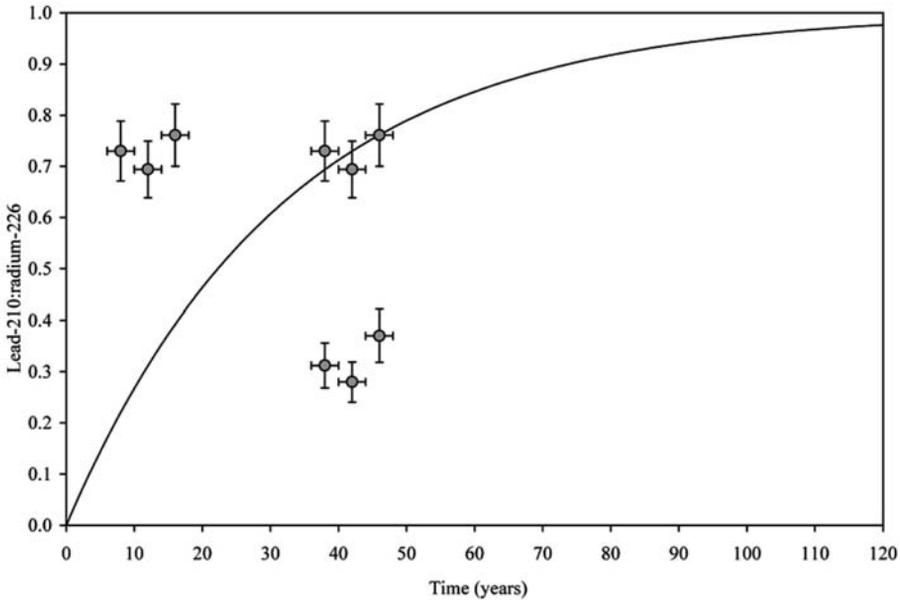
Fig. 1.   Diagrammatic representation of the theory behind lead-radium dating. Represented is the ingrowth of lead-210 from radium-226 as the ingrowth curve in the figure. The clusters of hypothetical data points represent the various forms of potential age differentiation from lead-radium ratios measured from samples with estimated age. The clusters not in agreement with the ingrowth curve represent scenarios where age was either underestimated or overestimated by several decades. The margin of error for age is typical for an age distribution from a pooled group of otoliths. The margin of error for lead-radium ratios is approximate for lead-radium activities that would be somewhat ideal. See Fig. 2 for a different graphic analysis of these same theoretical data examples.

Since this pioneering application, the technique has been applied to several other rockfishes with varying degrees of age resolution (Burton *et al*. 1999; Campana *et al*. 1990; Kastelle *et al*. 2000; Andrews *et al*. 2002, 2005, 2007; Stevens *et al*. 2004; Watters *et al*. 2006). Bomb radiocarbon dating of fish otoliths began in the southern hemisphere (Kalish 1993, 2001), followed by a series of studies in the northern hemisphere (e.g., Campana 1997; Kalish *et al*. 2001).

Lead-radium dating relies on the incorporation of naturally occurring radium-226 from the environment into the otolith and its subsequent decay to lead-210. By measuring the disequilibria of these two radioiso-topes in otolith core material (first few years of life), an independent estimate of age can be determined based on the known ingrowth rate of lead-210 from radium-226 (Fig. 1; Campana *et al*. 1990; Smith *et al*. 1991; Kimura and Kastelle 1995; Francis 2003). This technique works well as a tool for determining the validity of age interpretations that differ considerably, but its application is limited by relatively low resolution at ages approaching 100 years. Typically, the end result for this kind of study is support for, or refutation of, a given age estimation technique and establishment of an independent estimate of age or lifespan. For example, lead-radium dating performed on the yelloweye rockfish (*S. ruberrimus*) provided
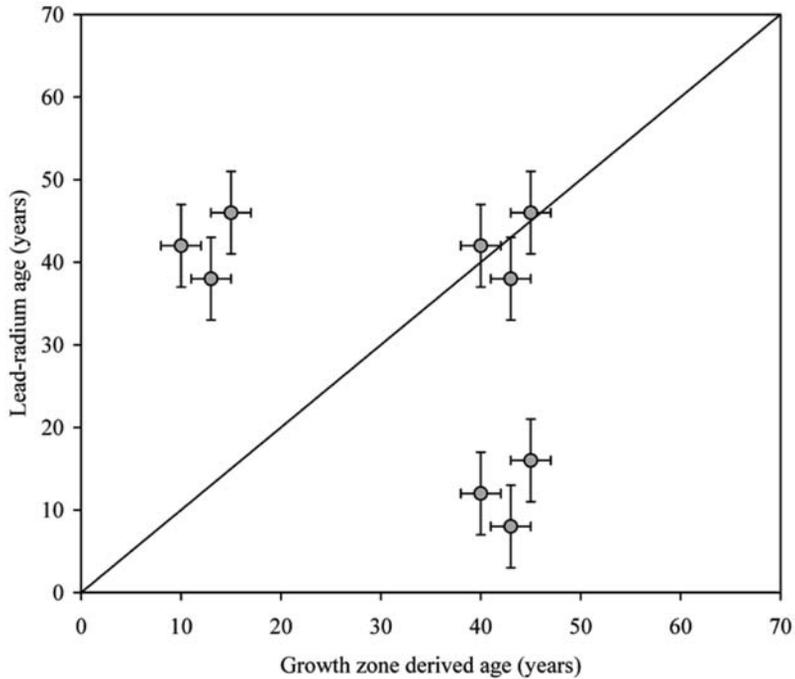
Fig. 2. Comparison of otolith-generated age estimate to radiometric age estimate using ratio of lead-210 to radium-226. The cluster of value on the line indicate that age estimates were confirmed by lead-radium age estimates, while those to the upper left mean that lead-radium ages were higher than growth zone derived ages. At the lower right the values indicate that otolith-derived ages were too high and lead-radium age estimates indicated that these samples were younger. See Fig. 1 for a different graphic analysis of these same theoretical data examples.

support for age exceeding ~100 yr (Andrews *et al*. 2002). The application refuted age estimates that were significantly younger and provided age validated support for transverse otolith ageing techniques, but this finding was the extent of the maximum age resolution because of technique limitations. These findings were similar for bocaccio rockfish for which a minimum age of 31 years was determined using lead-radium dating (Andrews *et al*. 2005).

Many papers now have been written on radiometric age determination of fishes since Bennett *et al*. (1982) first confirmed the longevity of the splitnose rockfish (*Sebastes diploproa*) using lead-radium dating. Such age validation studies usually involve two graphical comparison techniques. The first involves plotting the predicted ingrowth curve over time, plotted with individual age estimates (usually from growth zone counts in otolith sections), to determine the agreement between measured and expected lead-radium ratios (Fig. 1). The second approach is to plot the growth zone derived age estimates versus the radiometric age estimate for each sample (Fig. 2). With this kind of comparison, it is possible to test for trends of agreement or disagreement based on the hypothesis that there is a one-one agreement that results from a regression fitted to the data. The one discrepancy in this process that is still a work in progress is taking into consideration the change of radiometric age uncertainty with increasing age.

Use of the bomb radiocarbon chronometer requires a series of individual otoliths for which the birth years, based on standardized growth-zone age estimates, range from a time prior to significant atmospheric testing of thermonuclear devices (pre-1957) to the post-bomb period. This approach can utilize both the 1) time of first rise in radiocarbon, and the 2) sloped period for the rise in radiocarbon, as a time-reference markers for age validation. It is the agreement of the bomb radiocarbon record, from the species with age in question, with a reference bomb radiocarbon time-series that provides a basis for age validation. Hence, the utility of this approach for determining age or lifespan is dependent upon the difference between the collection year and time of first rise in radiocarbon for the reference time series. For example, a minimum lifespan of 43 ± 3 years was determined for canary rockfish (*Sebastes pinniger*) based on the first sample to have measured radiocarbon levels that were pre-bomb (Andrews *et al*. 2007). In addition, age can be determined by projecting measured radiocarbon levels back to a reference time series (Campana 1997); a minimum life span of 37 ± 2 years was determined in this manner for bocaccio rockfish (Andrews *et al*. 2005). A thorough evaluation of age classes can also be undertaken with a series of samples with different collection years (Piner and Wischniowski 2004).

For each of the three species discussed here, age has been determined using both lead-radium and bomb radiocarbon dating. Lead-radium results for yelloweye rockfish provided strong support for the age estimation criteria used to determine ages that exceed 100 years and the consistency of fit to the ingrowth curve for younger age classes provided additional support. Based on the ease of otolith reading for this species using the same criteria, we considered a radiocarbon record from otoliths of yelloweye rockfish would provide a reference chronology for validation of other regional fish species (e.g., Kerr *et al*. 2005). Some (e.g. Stewart and Piner 2007) have questioned this assumption and suggested that the follow up study using radiocarbon was instead further validation for the age estimate criteria and further support for the findings of the lead-radium study.

It seems there is an element of truth in both perspectives. Based on the findings of the combined studies, and depending on your perspective, the evidence that yelloweye rockfish is one of the longest lived rockfishes is robust. Lead-radium results for bocaccio rockfish provided only a minimum age for this species because of the remarkably low radium-226 levels; there was 95% confidence that the minimum age this species can attain is 31 years. This finding was well supported and exceeded with the application of bomb radiocarbon dating. Lead-radium and bomb radiocarbon results for canary rockfish worked well together by providing robust support for ages estimated in the Canadian canary rockfish fishery. Each application has had variable degrees of age validation based on the uncertainty or assumptions of the application, and there is still a need for developing a high-precision dating method.

Here, we stress the paramount importance that some form of validation or support be given for age estimation procedures, and ultimately estimates of longevity, before we can accurately understand the population dynamics of a population supporting a given fishery. Without determining the temporal periodicity of the growth zones in their otoliths, the variation in growth and longevity would not be fully understood for different species of fishes like bocaccio, canary and yelloweye rockfishes.

5. Deep-water Rockfish Age-Specific and Lifetime Reproductive Output

For the three species of interest here, we have provided age validated support using both lead-radium bomb radiocarbon dating (e.g.,
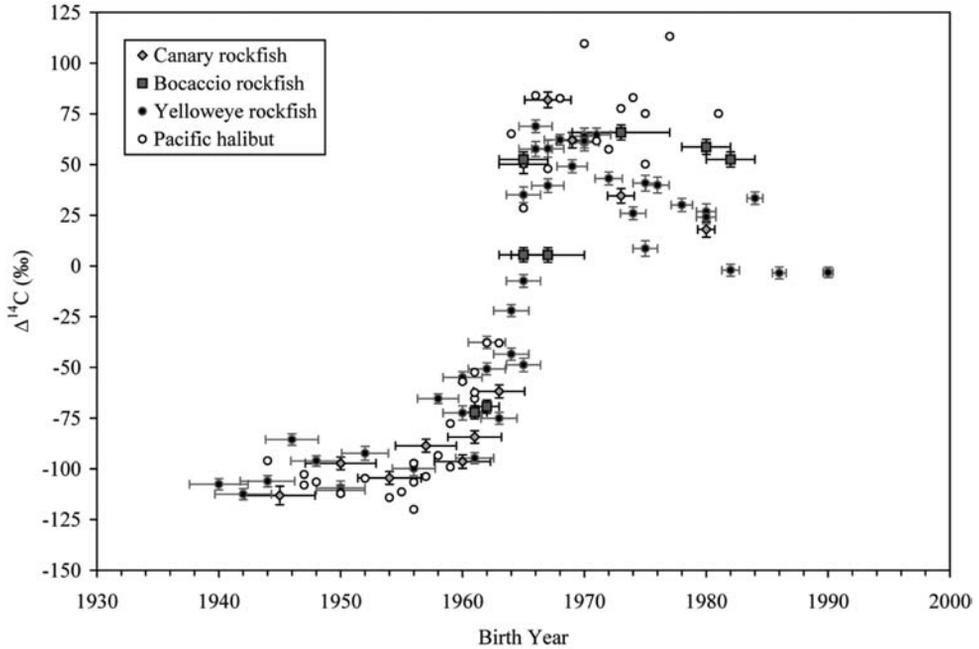
Fig. 3.   Plot of measured bomb radiocarbon ($\Delta^{14}C$) levels in otolith cores, representing the first year of growth, from adult bocaccio (*S. paucispinis*; Andrews *et al.* 2005), canary (*Sebastes pinniger*; Andrews *et al.* 2007), and yelloweye (*S. ruberrimus*; Kerr *et al.* 2005) rockfishes, plotted with $\Delta^{14}C$ data from whole otoliths of juvenile Pacific halibut (*Hippoglossus stenolepis*; Piner and Wischniowski 2004). Birth year was estimated using growth zone counts for both canary and bocaccio rockfishes and measured $\Delta^{14}C$ levels from each aged core was compared to the chronological reference time series established for the Northeastern Pacific Ocean; the chronological time series was established for the region with the age-validated yelloweye rockfish (Andrews *et al.* 2002) and known age juvenile Pacific halibut otolith records. Error bars for the data represent the analytical uncertainty of the $\Delta^{14}C$ measurements and the potential range for the birth date based on the age estimate uncertainty.

Fig. 3). For bocaccio, canary, and yelloweye rockfishes, the age estimates from otolith growth zone counts produced age estimates that conformed well to known regional bomb radiocarbon levels. Thus, age estimation procedures are independently supported for the estimated life spans of these three fishes and it is this supported life span that we propose is an important factor in determining the sustainability of fisheries.

This allows us to also feel confident that the resulting growth curves (Fig. 4 from Love *et al*. 2002) provide evidence of a variety of growth characteristics and life spans among many species of the genus *Sebastes*. Growth curves for 13 species of rockfishes, including yelloweye and canary rockfishes, are plotted in Fig. 4, but no growth curve was yet available for bocaccio when Love *et al*. (2002) published this figure. We now have a better idea of bocaccio growth, with best estimates, taken from MacCall (2007), of growth coefficients (K) ranging from 0.184–0.210, and asymptotic lengths (L_∞) being 75.9 and 65.6 cm TL, for females and males respectively. A life span estimate of ~50 years was used by Love *et al*. (2002). However, there is considerable variation in the value
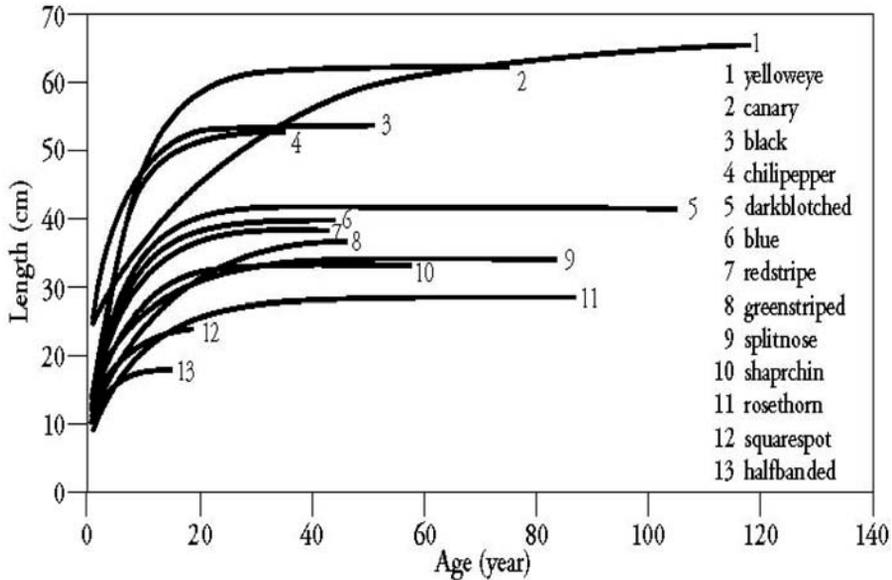
Fig. 4.   A compilation of data from numerous studies where von Bertalanffy growth curves were fitted to female length-at-age data (otolith section age) for 13 rockfish species. In the context of this study, the bocaccio growth data were not plotted because at the time of publication, age data was not yet resolved (Data and figure from Figure 9.6, page 61, in Love *et al*. (2002) with permission to reprint).

used for maximum age. MacCall (2007) reduced his maximum age estimate to 27 from 45 years used in his original 2003 stock assessment. Our most recent work indicates 37 ± 2 years for the largest fish used in the study (Andrews *et al*. 2005). Therefore, we feel the best estimate would be ~37 years based on our age-validated results, the importance of which will be discussed further.

A synopsis (Love *et al*. 2002) of fecundity information gathered from numerous studies has produced evidence that larger, and presumably older, rockfish females can provide maximum fecundities (number of eggs or number of larvae produced) that increase exponentially with maximum length (Fig. 5). Thus, the deeper-dwelling species, which are often larger, may have increased fecundity coupled with their increased longevity (Cailliet *et al*. 2001). The important question that comes from this observation

has to do with the number of years past age at maturity over which these females continue to produce eggs and larvae. In addition, both fishing and natural mortality can cause the relative numbers of females in successively older age classes to decline, further reducing their net reproductive rates over these years.

Knowing the longevity and age-specific fecundity for rockfishes allows us to speculate about the potential impact of size-specific mortality from fishing. Without fishing mortality, bocaccio, canary and yelloweye rockfishes would start spawning from the ages of approximately 7, 8, and 19 years, to the end of their lifetime at ages approaching 37, 84, and 118 years, respectively (Berkeley 2006; modified by our recent results). Hence, the longer-lived, deeper-dwelling canary and yelloweye rockfishes would have up to 76 and 99 reproductive years, versus up to 30
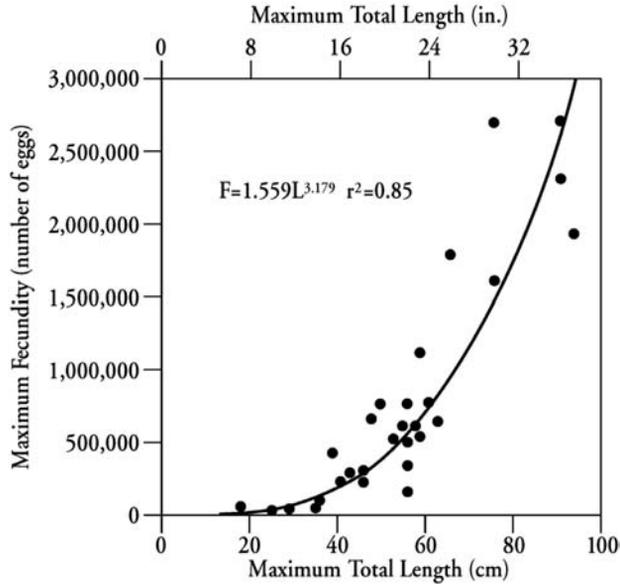
Fig. 5. A compilation of data used to establish a relationship between rockfish maximum length (*L*, cm) and fecundity (*F*) for 33 rockfish species from the eastern North Pacific (Data and figure from Figure 5.8, page 37, in Love *et al.* (2002) with permission to reprint). This relationship may be an indication that larger, and presumably older, fish are typically more fecund; typifying the concerns associated with size-specific management strategies.

years for the shallower, shorter-lived bocaccio rockfish. By taking this into consideration, it is relatively straight forward to predict that size-specific fishing mortality (i.e. heavily fishing the larger, older fish) would have a deleterious impact on lifetime egg (larval) production. This would be even more convincing if age-specific natural mortality, the growth rate and age at maturity were known.

Using this line of thinking, it is interesting to consider several other rockfishes that have greater life spans. The rougheye (*Sebastes aleutianus*) and shortraker (*Sebastes borealis*) rockfishes have estimated longevities ranging up to 157 and 205 years, respectively (Munk 2001); however, these estimates are based on growth zone counts from otolith sections. Niether lead-radium or bomb radiocarbon dating has been applied and the development of other tech-

niques is necessary to accurately ascertain ages of this magnitude. Assuming these estimates are accurate, these exceedingly long-lived fishes would be more vulnerable to size-specific fishing mortality that targets deep-dwelling individuals that are larger and potentially much older.

Likewise, age validation is an important factor in managing other long-lived fishes that are heavily exploited. For example, Baker and Wilson (2001) and Milton *et al.* (1995) validated longevities in snappers (family Lutjanidae) occupying relatively deep water in the Gulf of Mexico and off Australia, respectively. Another prime example, with a bit of a twist, is the orange roughy (*Hoplostethus atlanticus*) with its contrasting reproductive strategy of bestowal (maximizing investment in a smaller number of offspring; Pankhurst and Conroy 1987). This factor, combined with its validated

centenarian longevity (Fenton *et al.* 1991; Smith *et al.* 1995; Andrews and Tracey 2007), make orange roughy a particular concern in a size-selective management strategy. Other deep-water fishes with potentially high longevity, like oreos (family Oreosomatidae: Stewart *et al.* 1995), need to be further considered in this regard. This kind of vulnerability would be especially true for those targeted preferentially for egg production, like anglerfishes (family Lophiidae, genus *Lophius*: Duarte *et al.* 2001; Landa *et al.* 2001).

6. Conclusions

It is a combination of age structure (keep the big ones), life-time egg production (greater productivity), and genetic diversity (potential enhanced survivorship) that beg for further consideration of age validation and abandonment of only size-specific management practices. Age validation for fishes that are recognized as long-lived (e.g., Burton *et al.* 1999 and Cailliet *et al.* 2001), such as chondrichthyans (sharks: Cailliet and Goldman 2004; Cailliet *et al.* 2006), chondrosteans (sturgeon & paddlefishes: Burton *et al.* 1999), and tarpons (Andrews *et al.* 2001), either have required or will need to use a combination of techniques, including bomb radiocarbon, lead-radium dating, and/or tag-recapture and marking techniques to validate their growth characteristics and longevity estimates.

For chondrichthyan fishes and sturgeons, which are cartilaginous and do not have calcified otoliths that are useful, lead-radium dating did not work due to what appeared to be a violation of the closed system assumption (Welden *et al.* 1987; Burton *et al.* 1999). Radionuclides may move around from the vertebral column to the rest of the body, thus making lead-radium dating not useful for these fishes.

For some elasmobranch species, however, bomb radiocarbon dating has been suc-

cessfully applied because the signal is conserved in cartilage. Apparently, the bomb radiocarbon signal is conserved for some species, but may be: 1) free to move around in the vertebral column; or 2) mixed with radiocarbon-depleted sources in other species. This technique has worked well for the porbeagle (*Lamna nasus*: Campana *et al.* 2002), shortfin mako (*Isurus oxyrinchus*: Campana *et al.* 2002; Ardizzone *et al.* 2006), spiny dogfish (*Squalus acanthias*: Campana *et al.* 2006), and tiger shark (*Galeocerdo cuviei*: Kneebone *et al.* in press). It did not work as well for white shark (*Carcharodon carcharias*: Kerr *et al.* 2006).

In summary, both lead-radium and bomb radiocarbon dating provide solid, age-based evidence as tools in age validation of fishes. Lead-radium dating is useful for the groups of fishes with otoliths large enough, and with enough radioactivity, for core applications. Bomb radiocarbon dating has often corroborated age estimates, growth characteristics, and life spans of rockfishes, and deeper-dwelling species. Results so far indicate that these deep-water fishes can live a long time, and in a growing number of cases exceed a centenarian life span. As pointed out by Longhurst (2002, 2006), longevity is extremely important to insure effective, age-based management practices. In addition, the metabolism and growth of deep-water fishes appear to be lower and slower than near-shore fishes (Haedrich *et al.* 2001; Roberts 2002; Marriott *et al.* 2006; Drazen and Seibel 2007). Prevention of fishing down the larger and more productive age, not just size, classes is of paramount importance.

Acknowledgments

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