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# Spine-based ageing methods in the spiny dogfish shark, *Squalus suckleyi*: How they measure up



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## ABSTRACT

The second dorsal spine has historically been used for age determination in the spiny dogfish shark. The dorsal spines are located on the external surface of the body and are subjected to natural wear and breakage. Two methods have been developed to account for the worn portion of the spine and extrapolate the lost annuli. We compared the performance of these methods using a large data collection assembled from multiple sources, and evaluated their utility for stock assessment and management of the spiny dogfish shark *Squalus suckleyi* in the Northeast Pacific Ocean. Our results showed that the two methods produced very different age estimates for older fish with worn spines. Both methods raised significant questions about some aspects of the age estimates produced, and further exploration of techniques to account for worn spine annuli is needed. It is therefore important to develop alternative methods for shark age determination, including those using stained vertebrae.

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## 1. Introduction

Determination of fish ages is essential for assessment and management of fishery stocks to ensure the long-term sustainability of marine resources. Accurate age data enable reliable estimation of key life history parameters related to growth, natural mortality, and longevity, which are crucial for evaluation of current status and understanding the dynamics of a stock under alternative management scenarios (Campana, 2001; Cope and Punt, 2007; Gertseva et al., 2010; Hoenig, 1983).

The spiny dogfish shark is one of the most widely distributed sharks that inhabit temperate waters in both the Pacific and the Atlantic Oceans. Currently, two species of spiny dogfish sharks are recognized: *Squalus suckleyi*, which inhabits the North Pacific Ocean, and *Squalus acanthias*, which occurs outside of the North Pacific (Ebert et al., 2010). *S. suckleyi* has the longest gestation period known for sharks (22–24 months) with the number of pups in each litter ranging between 5 and 15 individuals. It is also the latest maturing (with 50% female maturity at age estimates ranging from 31 to 43 years) and longest lived of all elasmobranchs (Cortés, 2002; Gertseva and Taylor, 2011; Saunders and McFarlane, 1993; Smith et al., 1998; Taylor et al., 2013; Taylor and Gallucci,

2009). Such life history traits make the species highly susceptible to overfishing and slow to recover from stock depletion; its slow growth, late maturation and low fecundity are directly related to recruitment and spawning stock biomass (King and McFarlane, 2003).

Ages of teleost fish have been traditionally derived from hard structures, such as scales and otoliths, since these structures form annual growth marks that can be counted. Otoliths have been most extensively used, as they generally provide the most accurate ages, particularly for older fish (Boehlert, 1985; Boehlert and Yoklavich, 1984; Gertseva and Cope, 2011; Gertseva et al., 2010). Elasmobranch species such as sharks and skates lack hard structures, but it has been shown that vertebrae of most of these species deposit annual concentric growth bands (Gallagher and Nolan, 1999; Gertseva, 2009; Ketchen, 1975; Ridewood, 1921). Spiny dogfish sharks have distinct dorsal fin spines projecting from the body immediately anterior to each of two dorsal fins. The traditional method of estimating the age of dogfish has been to count the growth bands visible on the surface of their second dorsal fin spine (Kaganovskaia, 1933; Ketchen, 1975, 1986; McFarlane and Beamish, 1987). These bands are deposited annually; this has been validated using recaptures of tagged dogfish injected with oxytetracycline and bomb radiocarbon studies (Campana et al., 2006; McFarlane and Beamish, 1987). Vertebrae have not been widely used for ageing spiny dogfish. This may be due to a variety of factors including the smaller size of dogfish compared to many sharks, the ease of seeing the annuli on the dorsal

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spine, and difficulty in distinguishing bands within the vertebral centra.

The dorsal spines are subject to breakage and natural wear, when bands on the distal tip of the spine become indistinguishable. Two methods have been proposed to account for these lost annuli. Both methods involve statistical extrapolation based on several measurements of a spine. The first method was proposed by Ketchen (1975). Ketchen (1975) assumes that the relationship between spine diameter at the last readable point and the number of missing ages can be approximated by an exponential relationship between the base diameter and number of ages counted on the spines of younger dogfish that were determined to be unworn. The other method has recently been proposed by Cheng (2012). This approach assumes that the spine diameter grows according to a von Bertalanffy growth curve (von Bertalanffy, 1938) and estimates the number of missing ages as a random effect in a nonlinear mixed effects model fit to three diameter measurements along the unworn part of the dorsal spine. The Cheng method was proposed as an improvement to the Ketchen method, as the use of multiple measurements along the spine and accounting for individual variability in spine growth are potentially valuable additions in calculating the number of lost annuli.

Both methods for extrapolating missing dogfish shark ages from measurements of dorsal spines have potential issues. The Ketchen method was developed from young spiny dogfish that exhibit clear and easy to read bands on their spines, and it was suggested that criteria developed from younger (presumably faster growing) fish could lead to underestimation of ages when applied to older individuals (Cheng, 2012; McFarlane and Beamish, 1987). The Cheng method, on the other hand, was developed from a limited number of samples (67 males and 115 females) and has not yet been widely applied.

The objective of this study was to compare the results of both methods applied to new data, collected on the West Coast of the United States, and evaluate their utility for stock assessment and management of spiny dogfish shark in the Northeast Pacific Ocean. For the analysis, we used a large collection of data on dogfish lengths and spine measurements assembled from multiple sources. We present the results of our application of these methods, discuss the advantages and shortcomings of each one, provide explanations for patterns observed in age data generated by both methods, and finally provide recommendations on how to improve reliability of age estimates for spiny dogfish in the future.

## 2. Materials and methods

Dogfish spines were collected in the Northeast Pacific Ocean, in the coastal waters off Washington, Oregon and California. Several sources were used to generate age data analyzed in this study. The Washington Department of Fish and Wildlife (WDFW) has continuously collected dorsal spines from spiny dogfish landed by commercial fisheries since 2003. These fisheries included bottom trawl, mid-water trawl and logline fisheries targeting variety of economically valuable species, but taking dogfish as bycatch. Second, spiny dogfish are one of most common bycatch species in the US West Coast mid-water trawl fishery targeting Pacific hake (Gertseva and Taylor, 2011), and the National Marine Fisheries Service (NMFS) At-Sea Hake Observer Program (A-SHOP) has continuously collected dogfish age data from this fishery since 2007. Finally, we had age samples from 2010 NMFS Northwest Fisheries Science Center (NWFSC) ground-fish bottom trawl survey conducted on the shelf and slope of the Northeast Pacific Ocean (Bradburn et al., 2011). In total, we had data from 4841 dogfish, including 4257 samples from commercial fisheries starting in 2003, and 584 samples from bottom

**Table 1**

Sample sizes of age data used for the analysis by sex and data source.

	Bottom trawl	Mid-water trawl	Longlines	NMFS survey	Total
Females	181	1224	762	296	2463
Males	144	1417	529	288	2378
Total	325	2641	1291	584	4841

trawl survey. Males and females were of similar sample sizes (Table 1).

The data for all samples were compiled by WDFW and included sex, total length, and a collection of measurements from the second dorsal spine. The spine measurements included: a determination of whether or not annuli were missing due to wear (worn/unworn), the diameter of the spine measured in 3 places (base, last readable point, beyond which annuli are no longer visible, and an intermediate location), and a count of the annuli between each of the points where spine diameter was measured. The location of points used for spine diameter measurements are described in details in Ketchen (1975) and Cheng (2012).

The majority of spines used in this analysis included some annuli that have been worn and can no longer be counted. For these worn spines, WDFW also provided age estimates from applying the Cheng (2012) method, while ages from Ketchen (1975) method were generated by the authors. To illustrate his method and estimate parameters to extrapolate missing ages, Ketchen used dogfish collected in British Columbia waters, and noted variability in parameter estimates in fish collected from different locations (Hecate Strait vs. Strait of Georgia). We used the same general approach proposed by Ketchen to determine ages of dogfish caught off the US West Coast and estimated new parameter values, since our data are from potentially a different population, in a different geographic location, and time period (50–60 years later). Furthermore, the method of counting bands on dogfish spines was refined by McFarlane and Beamish (1987) after recaptured dogfish with oxytetracycline marking indicated that methods at the time of Ketchen (1975) undercounted some of the bands. Thus, the parameter values estimated in this analysis are not expected to be comparable to those estimated by Ketchen (1975).

The method of accounting for missing ages proposed by Ketchen (1975) assumes that the relationship between spine diameter at the last readable point and the number of missing ages can be approximated by the relationship between the base diameter of a spine and number of ages counted on the spines of younger dogfish that were determined to be unworn. Ketchen modeled this relationship using the equation:

$$Y = \alpha X^\beta \quad (1)$$

where  $X$  is the spine base diameter in millimeters,  $Y$  is the estimated age in years from conception (assumed to be the age since birth +2), and  $\alpha$  and  $\beta$  are parameters controlling the scale and curvature of the estimated curve. Parameters  $\alpha$  and  $\beta$  are estimated by applying a linear model to the data on a log–log scale under the assumption that,

$$\log(Y_i) = \alpha + \beta \log(X_i) + \varepsilon_i \quad (2)$$

where  $\varepsilon_i$  is a normally distributed error term. In estimating the parameters on this log–log scale, we assume that the variability in annuli count around the expected value is greater for larger spines than for smaller, a pattern which is supported by the data. Ketchen (1975) described using “functional regression” which could take into account variability in the diameter measurement in addition to the assumed variability in the dependent variable. However, there is no indication that such uncertainty was included by Ketchen (1975). Furthermore, double readings of the caliper measurement



indicated very little uncertainty in this measurement. Thus, simple linear regression was used in this analysis.

We used 513 unworn spines to calculate parameter values for the Ketchen method. This included 260 samples from commercial fisheries and 253 from the 2010 NWFSC survey. The use of spines that were truly unworn represents a modification of the approach used by Ketchen, who included spines with a diameter at the no-wear point of less 2.05 mm, “the calculated average diameter of the spine base 1 year after birth” (Ketchen, 1975). Including spines with minimal wear increases the range of base diameters in the regression, but also introduces potential for bias due to the inclusion of a few samples with slower growing spines that may have an unknown number of missing ages that is potential greater than 1 year as assumed by Ketchen.

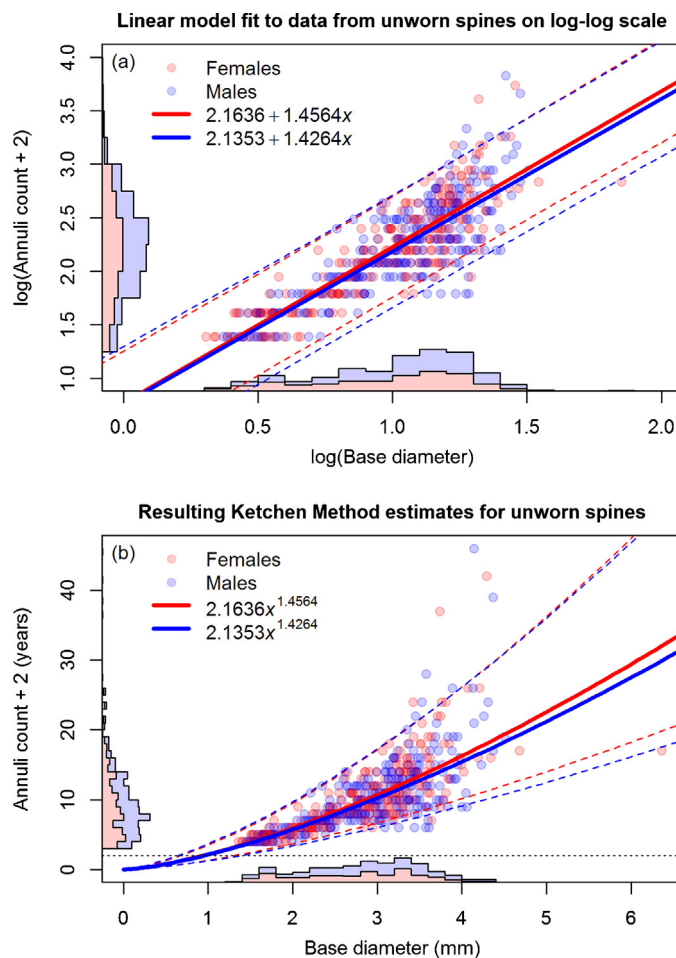
The linear model was estimated in R (R Development Core Team, 2012), which was also used to estimate predictive intervals. We estimated separate parameters for females and males based on the *a priori* assumption that two sexes have different growth rates, even though the estimated parameters for females and males were not significantly different from each other (at the  $\alpha=0.05$  level).

The Cheng (2012) method for extrapolating the number of missing ages on worn spines assumes that the spine diameter grows according to a von Bertalanffy growth curve (von Bertalanffy, 1938), which is a reasonable assumption given that a strong correlation ( $\rho=0.95$ ) between spine base diameter and fish length was observed in data we used for this analysis. The estimates of the number of missing ages in the Cheng method are calculated as a random effect in a nonlinear mixed effects model fit to three diameter measurements along the unworn part of the dorsal spine (Cheng, 2012). In this model, the random effect is used to account for the unknown number of missing ages, not individual variability in growth rates. The Cheng parameters, used by the WDFW to extrapolate the number of missing annuli, were derived from samples collected on 115 females and 67 males landed by commercial fisheries in Washington State ports. A separate set of parameters was estimated for each sex.

To evaluate uncertainty in spine measurements and in annuli count of the readable portions of spines, we examined measurements from the same 98 spines, but conducted by two different age readers (double reads). However, only the single readings of spines were used to estimate parameters for both methods (no double reads).

### 3. Results

The estimated parameters for the Ketchen method of extrapolation for worn spines were  $\alpha = 2.1636$ ,  $\beta = 1.4564$  for females, and  $\alpha = 2.1353$ ,  $\beta = 1.4264$  for males (Fig. 1). There was high variability in the relationship between the numbers of annuli counted and base diameter measurements for the 513 unworn spines used in this estimation, so the 95% predictive intervals indicated a large uncertainty in the extrapolation using the Ketchen method. The mean spine diameter at birth was estimated to be just under 1 mm. The predictive intervals (in ages since birth) for a spine with a last readable point of 3 mm were 4.7–15.2 years for females and 4.1–15.3 years for males. For a last readable point of 4 mm, the intervals were 8.2–24.1 years for females and 7.1–24.1 years for males. Of the 4213 worn spines with a last readable point recorded, 29% of the diameters at that point were 3 mm or greater and 9% were 4 mm or greater. The 95% predictive interval associated with the 2.05 mm criteria used in the original Ketchen (1975) analysis for inclusion in the parameter estimation is 1.8–7.9 years for females and 1.5–8.1 years for males. Predictive intervals were not available for the ages estimated using the Cheng method.

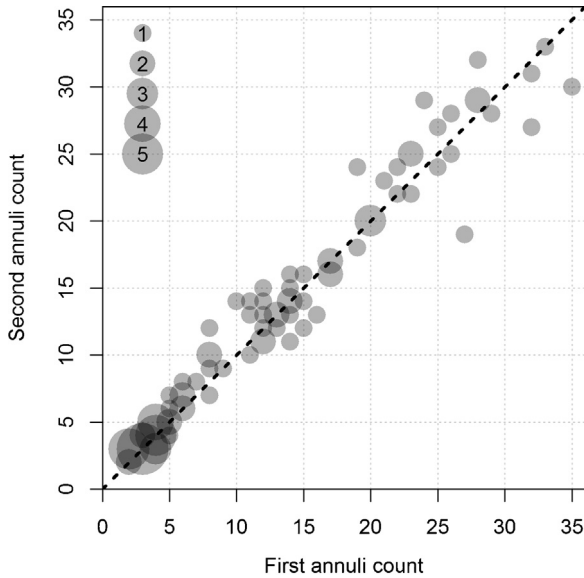


**Fig. 1.** Fits of the estimated Ketchen method relationship to the base diameter and annuli counts of unworn spines. Histograms at margins indicate marginal distributions of points. Solid lines estimated models for males and females on log–log scale (a) and natural scale (b). Dashed lines show 95% predictive intervals calculated from each model.

The range of the predictive intervals from the Ketchen method of estimating the unreadable portion of the spine is much greater than the uncertainty in the annuli count of the readable portion, where only 1 out of 98 double readings had a difference of greater than 5 years between readings (Fig. 2). Multiple measurements of the spine diameter at the last readable point also showed very little difference between measurements, with a maximum difference of 0.06 mm.

We found clear differences between age estimates produced by the two extrapolation methods for fish with worn spines. The maximum ages for Ketchen and Cheng methods were estimated as 71 and 90 years, respectively. Of 1043 fish with length greater than 80 cm, the mean difference between ages between Ketchen and Cheng was 12.4 years.

The methods also differ in how they treat extrapolated annuli at the outset between those determined from the directly read unworn spines and those with extrapolated annuli (Fig. 3). The Ketchen method estimates a mean spine diameter of about 1 mm at birth. Thus, spines with a diameter less than about 1 mm at the last readable point are estimated to have no missing ages (Figs. 1 and 3). In contrast, the smallest estimated values for the number of missing ages from the Cheng method are 3.4 years for females and 6.4 years for males (Fig. 3). This difference translates into inconsistencies between directly read and extrapolated ages for the Cheng method (Fig. 4). In the bottom two panels of Fig. 4, ages which were directly read from unworn spines form separate clouds from ages estimated



**Fig. 2.** Annuli counts from double reads of unworn portion of 98 dogfish spines. Area of circle corresponds to number of samples at that combination of values. Numbered circles in upper left indicate sizes associated with 1–5 samples at given combination.

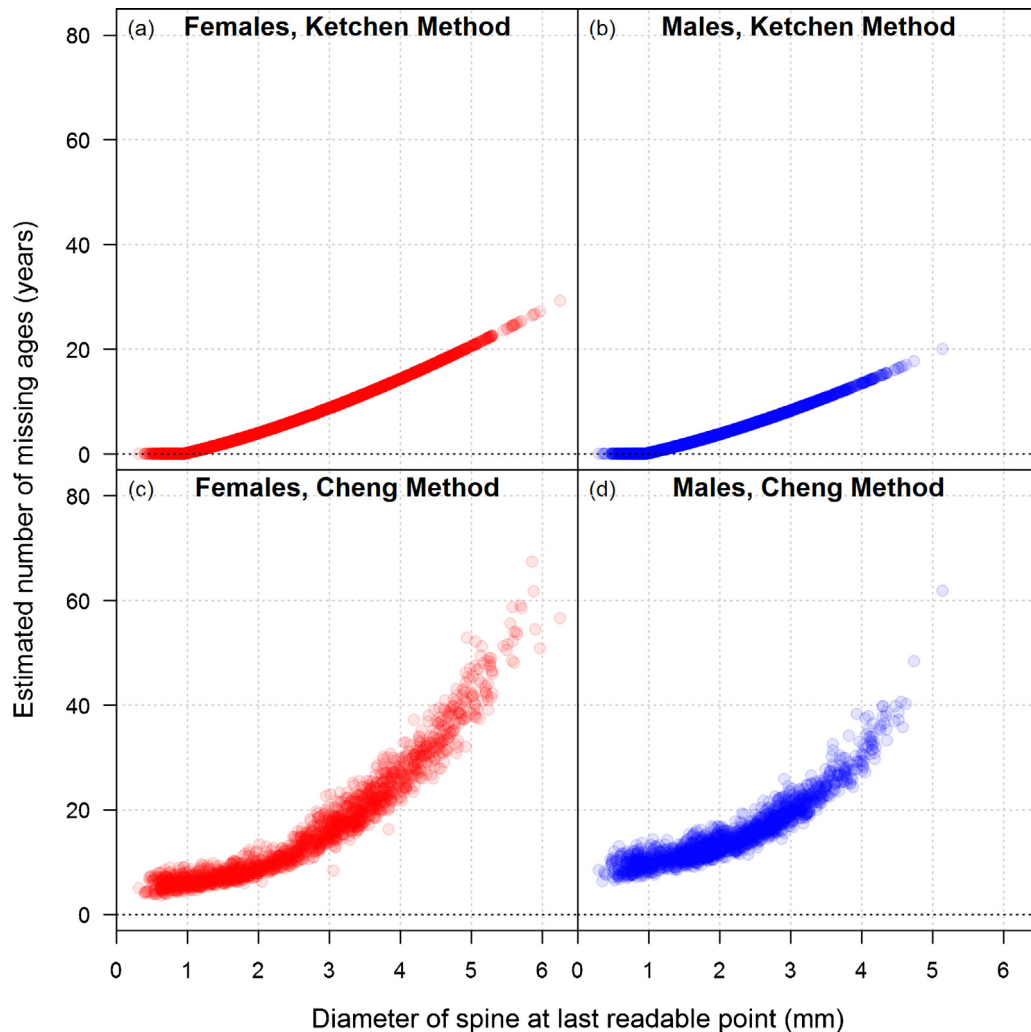
via Cheng extrapolation with worn spines. The distribution of age at length also reflects strong differences between worn and unworn spines, particularly for the Cheng method (Fig. 5). For example, of the 205 age samples from male dogfish with length between 45 cm and 50 cm, the mean age of the 70 fish with unworn spines was 9.3 years, whereas the mean estimated age associated with the 135 worn spines was 11.3 years when estimated by Ketchen method and 17.2 years when extrapolated by Cheng method.

The pattern of female length at age data (left panels in Fig. 5) does not appear to follow a von Bertalanffy function well for either age method. Larger females form a separate group that does not fit into the growth curve suggested by smaller individuals. Also, for both methods, it is evident that length at age data exhibit a similar pattern where a range of female lengths are conspicuously rare in comparison with the other lengths in the distribution.

Finally, in the Cheng method, the slope of the age–length relationship appears quite different for directly read (unworn) ages, than for extrapolated (worn) ages, for both males and females. In contrast, ages derived from worn and unworn spines appear to both follow the same function in Ketchen (Fig. 5).

#### 4. Discussion

The second dorsal spine has historically been utilized for age determination in the spiny dogfish shark (Campana et al., 2009; Cheng, 2012; Holden and Meadows, 1962; Ketchen, 1975;



**Fig. 3.** Estimated number of missing ages on worn dogfish spines calculated from each extrapolation method related to the diameter of the last readable point.

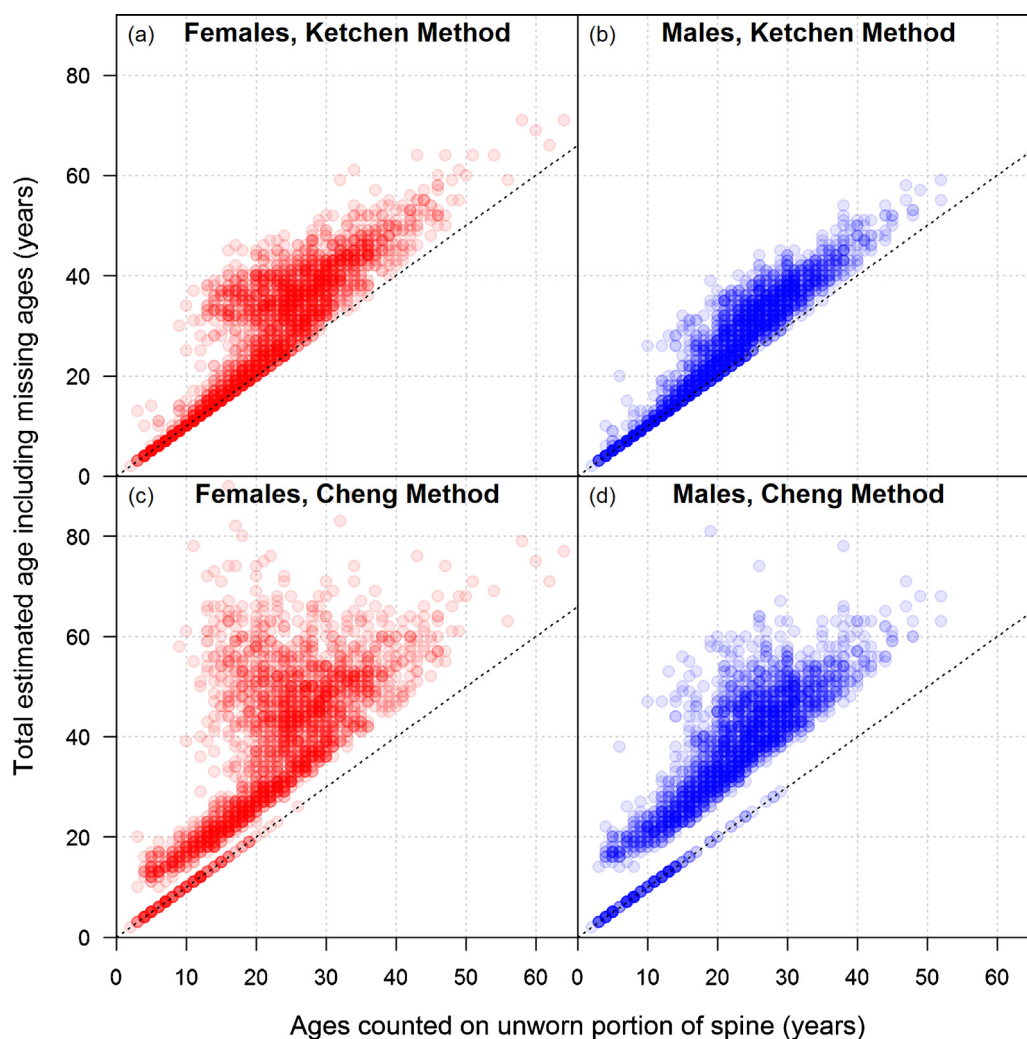


Fig. 4. Total estimated age vs. the number of ages countable on the spine for males and females from each method of age determination.

McFarlane and Beamish, 1987). The dorsal fin spines are located on the external surface of the body and are subjected to natural wear and breakage. Methods have been developed to account for the worn portion of the spine and extrapolate the missing annuli in order to estimate spiny dogfish ages (Cheng, 2012; Ketchen, 1975). We evaluated the performance of these methods, using spines of North Pacific spiny dogfish *S. suckleyi* collected from commercial fisheries, and within the NMFS bottom trawl survey in the Northeast Pacific Ocean.

#### 4.1. General findings

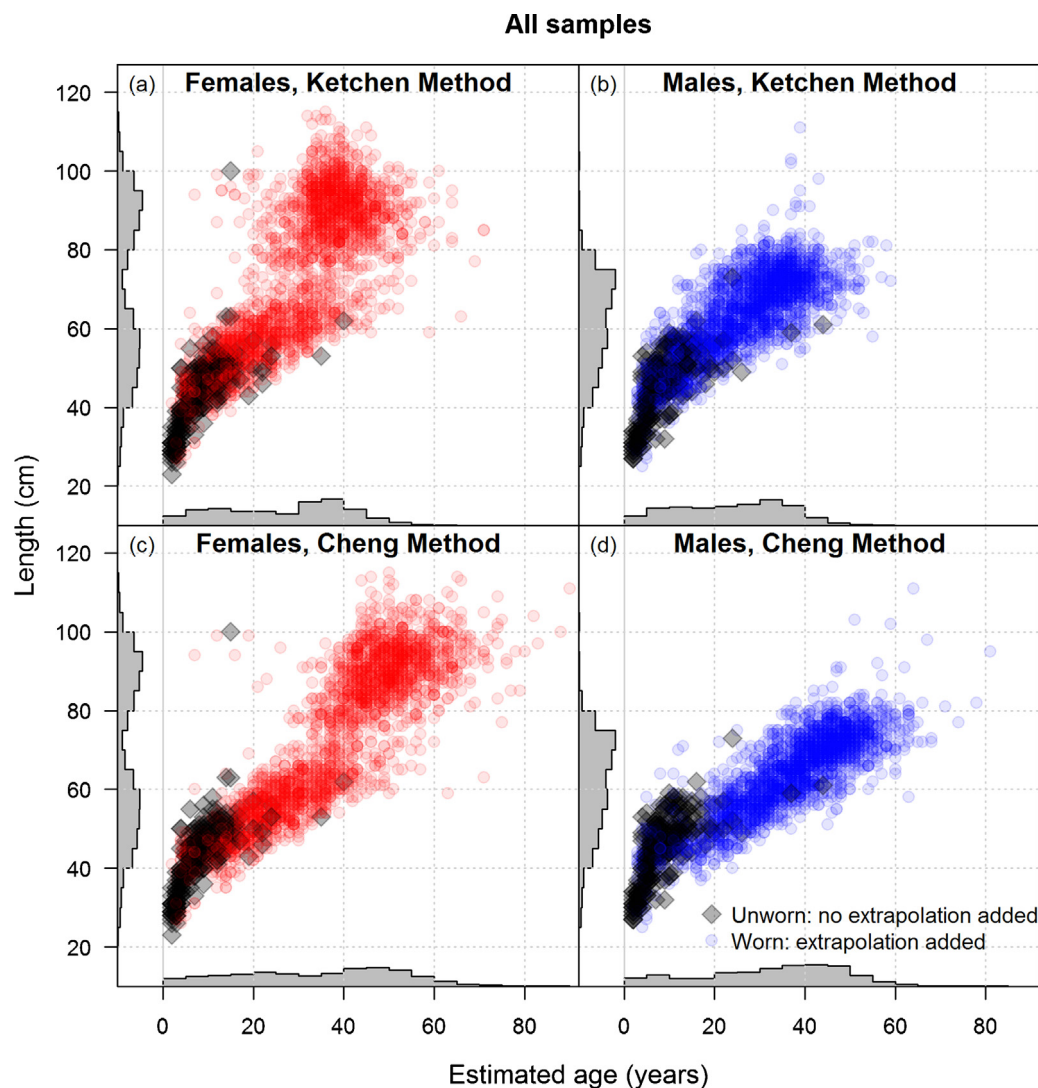
Our results showed that the two methods produced very different age estimates for older fish when missing ages were determined via statistical extrapolation. Extrapolation is based on measurements of spine diameter at several locations along the spine. Double readings of annuli on the unworn portion of a subset of the spines and double measurements of spine diameter for this same subset indicated that uncertainty in the annuli counts and discrepancies in measurements of spine diameter were very small compared to the uncertainty within and between methods of estimating the missing annuli on the worn portion of the spine.

Both methods raised questions about some aspects of the age estimates produced. In the Ketchen method, the statistical extrapolation does not account for natural variability between individuals in spine growth and thus predictions made from the mean

relationship are highly uncertain, with wide prediction intervals. Also, the exponential model may not be biologically realistic, as the high correlation between fish length and spine base diameter suggests that the von Bertalanffy model may be a better choice for growth in spine diameter than the exponential model. The unworn spines with the largest base diameters were those for which the exponential model fit the worst (Fig. 1), suggesting that the Ketchen method estimates of age for dogfish with the most wear on their spines are likely to be biased low. In the original application, Ketchen (1975) included spines with minimal wear in estimating the extrapolation relationship. However, the upper limit of the 95% prediction interval for a spine with last readable point of 2.05 mm (the cutoff used in the original analysis), is about 8 years. Even worn spines with a diameter of only 1 mm at the last readable point have some potential to have more than 1 missing annulus. Thus, in our application of this method, for which we had larger sample sizes, we chose the cleaner approach of using only unworn spines.

The Cheng method uses the more biologically sensible von Bertalanffy model and offers a number of potential improvements to the process of account for missing ages on worn dogfish spines, including the use of multiple diameter measurements and a more sophisticated statistical method based on random effects. However, our results highlight some concerns about the methodology and the resulting distribution of dogfish length at age using estimates based on this new method that suggests potential biases. The ages which were directly read from unworn spines





**Fig. 5.** Age vs. length for males and females from each method of age determination. Histograms at margins indicate marginal distributions of points.

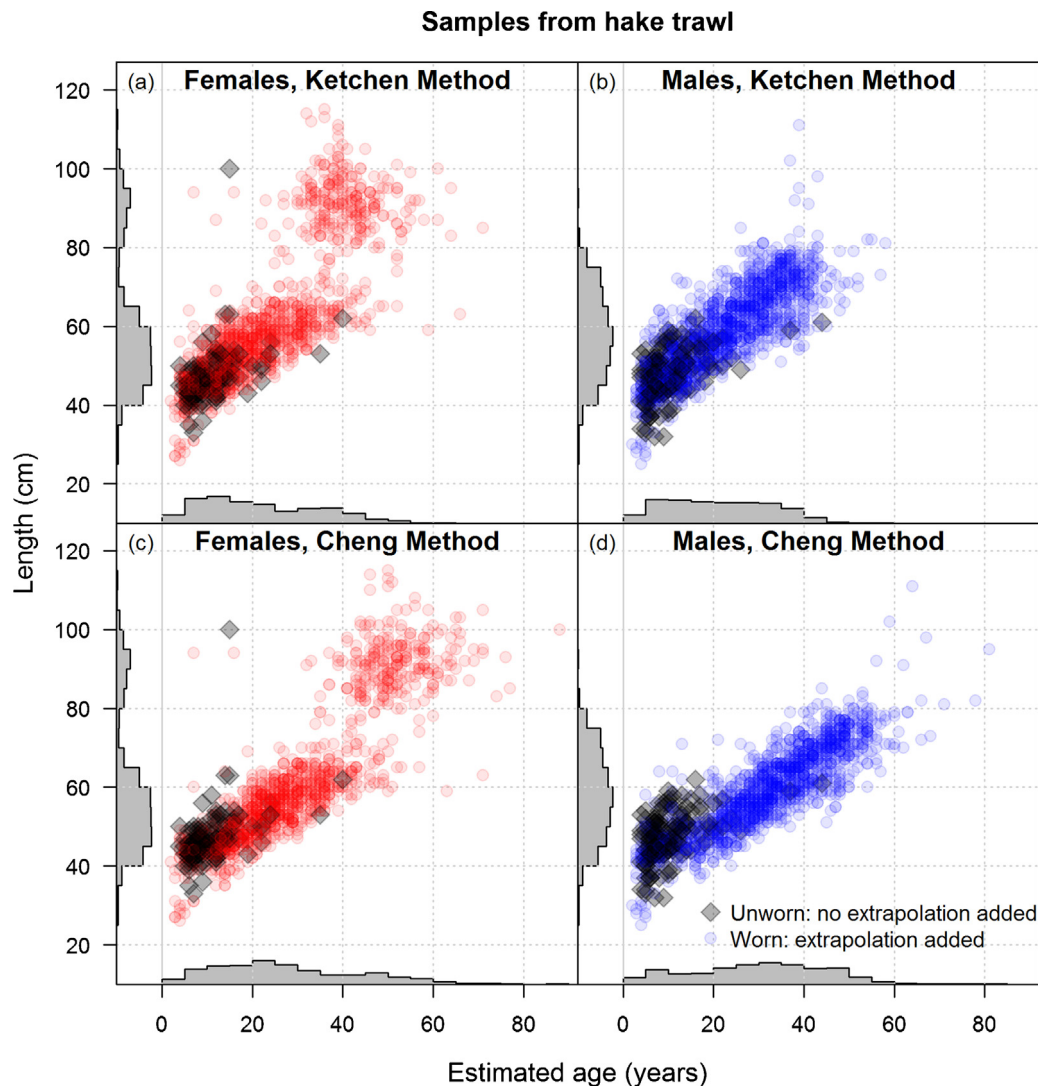
were completely separated from ages estimated via extrapolation; a 3-year gap for females and a 6-year gap for males was produced between ages determined from unworn spines and those with extrapolated annuli. This resulted in extrapolated ages being clearly biased higher than directly read ages (Figs. 3 and 4). Such a gap can be explained in part by the fact that Cheng (2012) does not take into account a two year gestation period when estimating ages from the worn spines, and thus counts ages from conception rather than from birth. Also, in the Cheng method, ages of females and males (males in particular) from worn spines with the extrapolation applied (blue dots on Fig. 5) followed a very different slope compared with ages from unworn spines (black dots in Fig. 5), again indicating inconsistencies between extrapolated and non-extrapolated ages. The Cheng method treats missing ages as a random effect, but does not consider individual variability in growth. That is, spine diameter for all specimens is assumed to grow according to the same von Bertalanffy curve. Thus, spines, which grow faster or slower than average, may have biased values in the number of missing ages assigned to them.

#### 4.2. Explaining “missing” females in length at age distribution

For both methods, it was evident that length at age distribution exhibited a similar pattern, where a range of female lengths

were conspicuously rare in comparison with the other lengths in the distribution (Fig. 5). This gap in lengths could be the product of sampling effects, since the majority of the length measurements were taken from the mid-water trawl fishery that targets Pacific hake (Table 1). It has been documented that younger individuals of spiny dogfish (10–15 years, with lengths up to 60 cm) concentrate in pelagic water and move to demersal habitat to mature when they are from 50 cm to 80 cm in length (Beamish and Sweeting, 2009). Larger dogfish also occur in the pelagic waters but they are less numerous than younger individuals (Beamish and Sweeting, 2009). It would be, therefore, reasonable to expect a bimodal distribution for lengths associated with this fishery. To explore this hypothesis, we examined the distribution of length samples taken from different gear types and found that although a paucity of female lengths between 65 cm and 75 cm is most obvious in the samples from the mid-water trawl fishery (Fig. 6), it is also apparent, although to a smaller degree, for bottom trawl survey catches (Fig. 7). Male samples do not follow the same pattern when lengths of a particular range are missing (Figs. 5–7).

There are several possible explanations for the lack of individuals of particular size range in a population. It could reflect either the impact of a fishery selecting a particular size group in a population or a poor recruitment period; it could also be related



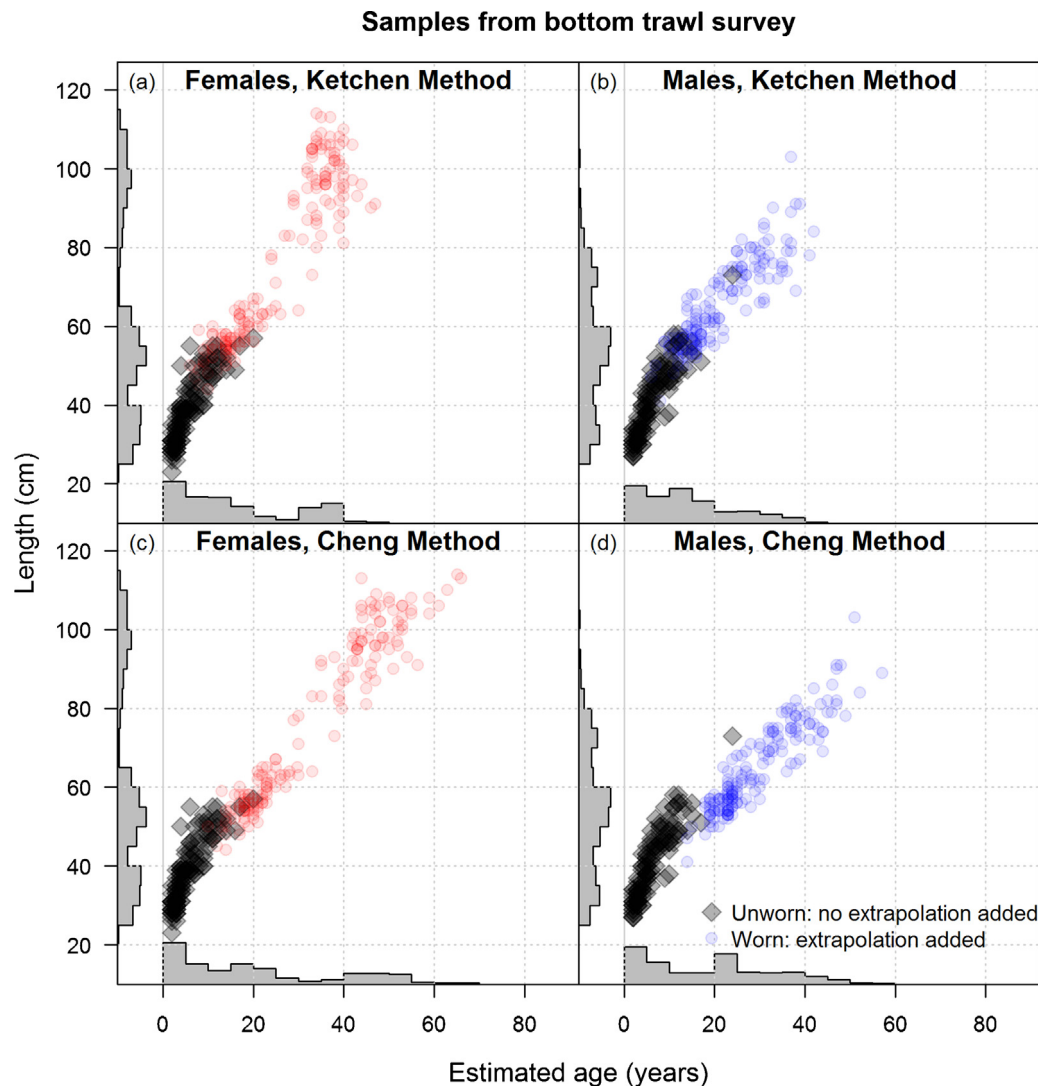
**Fig. 6.** Age vs. length for males and females caught by mid-water trawl gear from each method of age determination. Histograms at margins indicate marginal distributions of points.

to behavioral traits of the species with a particular size group being unavailable for fishery and survey gear. The history of dogfish utilization included a brief but intense fishery in the 1940s, which started soon after it was discovered that livers of spiny dogfish contain high level of vitamin A (Alverson and Stansby, 1963; Bargmann, 2009; Ketchen, 1986). However, since 1950, when the vitamin A fishery ended, spiny dogfish has not been a highly prized and targeted product, and estimates of total mortality, including bycatch in other fisheries, are low compared to the landings in the 1940s (Gertseva and Taylor, 2011). Furthermore, data collected in the early 1940s, prior to the peak of the fishery, also showed a similar bimodal length distribution for female dogfish in coastal waters (Taylor and Gallucci, 2009). It is therefore unlikely that this fishery would be responsible for removals of 65–75 cm individuals, a length that corresponds to 30–40 years of age. Poor recruitment is also insufficient to explain an apparent lack of exclusively females, which is the pattern in the large number of samples we analyzed from multiple fishery dependent and independent sources (Figs. 5–7). A poor recruitment period would be translated into both genders of particular ages (sizes) missing. Besides, spiny dogfish are considered *K*-strategists (Pianka, 1970; Roff, 1992), producing few, but relatively well developed offspring, not highly

susceptible to environment-driven juvenile mortality (King and McFarlane, 2003; Gertseva and Taylor, 2011).

A more probable explanation, therefore, is that this anomaly in the distribution of observed lengths could be due to a sex and size-specific behavioral difference in occurrence by habitat type (such as bottom relief), migratory behavior, or place in the water column. Segregation by size and sex has been reported for a number of shark species, including lesser spotted dogfish (*Scyliorhinus canicula*), spurdogs (*S. acanthias*), white-tip sharks (*Carcharhinus longimanus*) and scalloped hammerhead sharks (*Sphyrna lewini*) (Backus et al., 1956; Compagno, 1984; Ford, 1921; Klimley, 1987; Sims, 2003; Springer, 1967; Wearmouth et al., 2003). Spatial segregation between sexes and among size groups may be caused by differences in swimming speed, dietary preferences, and lack of aggression among sharks of same sex and similar size. Females of the lesser spotted dogfish (*S. canicula*), for example, take refuge in shallow water caves during the day and forage nocturnally every second or third night, while males remain active day and night and forage nightly in deep water (Wearmouth et al., 2003). Sex-specific migratory behaviors have been observed in the spiny dogfish (*S. acanthias*), a close relative of *S. suckleyi*, where individuals travel in dense groups, comprised of one sex, and are rarely found in





**Fig. 7.** Age vs. length for males and females caught by the bottom trawl survey from each method of age determination. Histograms at margins indicate marginal distributions of points.

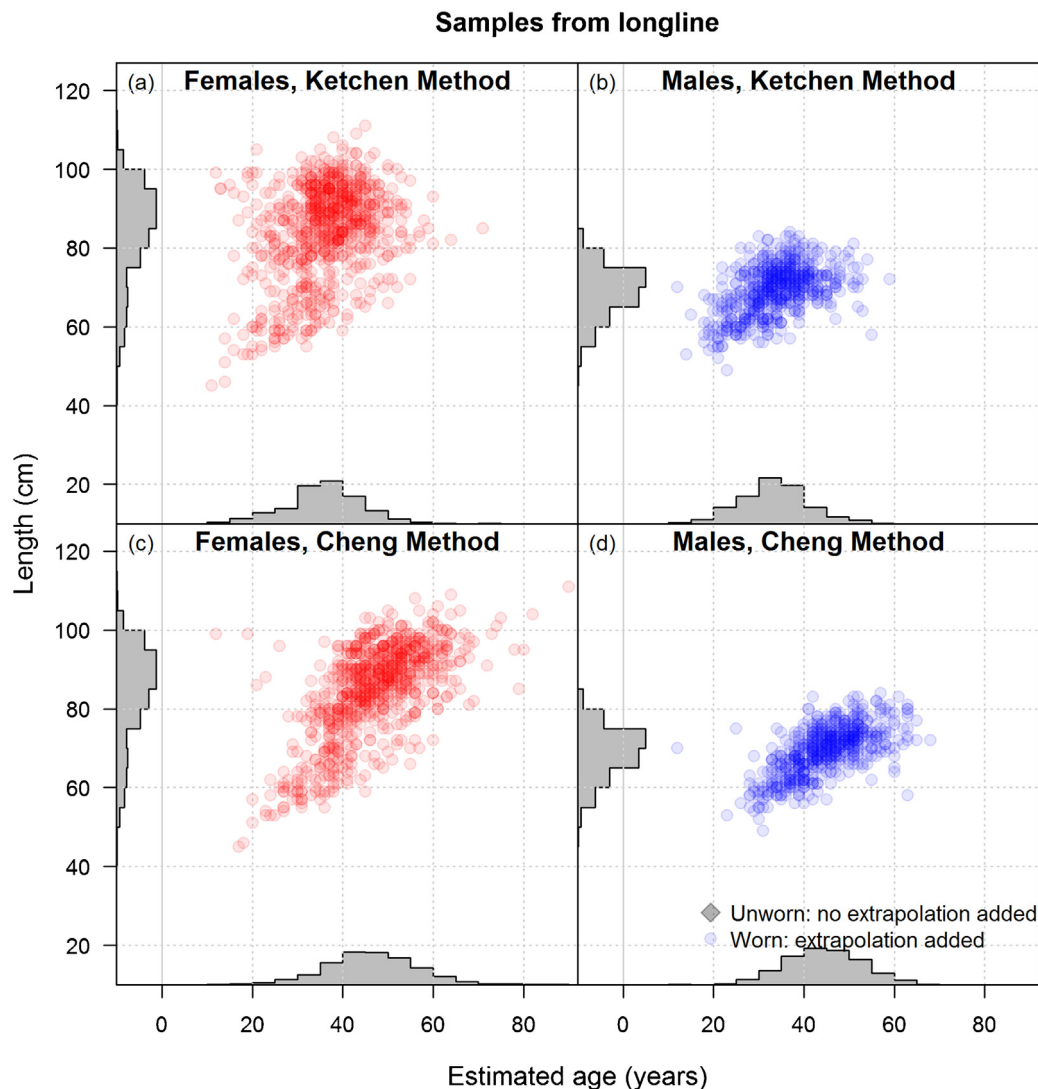
mixed sex groups (Jensen, 1966; Ketchen, 1986). Sex and length-class dependent habitat preference has also been demonstrated in *S. acanthias* in US and Norwegian waters (Hjertnes, 1980; McMillan and Morse, 1999; Shepherd et al., 2002), and mature *S. acanthias* have been shown to occupy inshore habitats more than immature individuals (Hurlbut et al., 1995; Nammack et al., 1985).

Given the widespread occurrence of sex- and size-specific segregation by habitat in many sharks (Clarke et al., 2001; Coelho and Erzini, 2010), and in a close relative, it is reasonable to infer that such a mechanism could be responsible here, with *S. suckleyi*. We saw that the paucity of females in the 65–75 cm length range was wider and more pronounced in mid-water and bottom trawl fishery and survey catch, and was much narrower and less noticeable in longline samples, which can access rocky, untrawlable habitat (Fig. 8). This could imply that females within that size range frequent rocky habitats more than other areas. *S. suckleyi* may exhibit sexual segregation somewhat similarly to scalloped hammerhead sharks, where it has been proposed that sexual segregation occurs through female-mediated choice for rocky habitat (Klimley, 1987; Sims, 2003). However, this hypothesis should be further explored as our findings are likely to be confounded with gear selectivity patterns.

#### 4.3. Explaining female pattern in length at age relationship

For either ageing method, female length-at-age data also do not appear to follow the von Bertalanffy function well (Fig. 5). Larger females form an odd cloud shape of length at age estimates that do not fit into the growth curve, implying that ages of larger individuals might be underestimated by both methods, with the degree of age underestimation increasing with age in the larger females. It is notable that the cloud of aberrant points for both methods lies largely beyond the 88 cm estimated length at which 50% of female spiny dogfish shark are mature (Taylor and Gallucci, 2009).

This peculiar pattern in female length at age data might be explained by a change in spine allometry related to female reproduction. A physiological explanation for such a change is that during pregnancy, materials needed for spine growth are also used for production of developing embryos (and their egg cases, made of similar material as spines), and thus maternal spine growth is temporarily retarded, due to re-allocation of resources to build egg cases for the young. A similar phenomenon is seen in humans, where maternal bone density diminishes during pregnancy, and its extent is highly correlated with baby birth weight (Yoneyama and Ikeda, 2000). A reduction in the rate of spine growth during pregnancy would



**Fig. 8.** Age vs. length for males and females caught by longline gear from each method of age determination. Histograms at margins indicate marginal distributions of points.

translate into a population level average reduction in annulus width following the age of maturity, which could produce the pattern observed in female length at age data in Fig. 3. Dogfish second dorsal spines used for age determination by both Ketchen and Cheng methods begin to wear when fish are about 20 years old, when most dogfish are immature. Therefore the spines of mature individuals are often worn beyond the point from where narrowing of the bands would begin, so the relationship between spine diameter and the number of missing ages derived from unworn spines, which were collected from immature individuals, might not be applicable for mature females. Therefore, further exploration of statistical techniques to account for worn annuli to improve reliability of age estimates particularly for mature females is warranted.

Estimating parameters for extrapolating missing ages for mature and immature females separately is one way to account for differences between mature and immature females in the relationship of spine diameter with number of missing ages, and thus improve the fit for female length at age data overall. A reduction in average annual spine growth rate at a particular age could likely be measurable by comparing width of annuli over the length of the spine in immature and mature females. The process of estimating the point of change in average annulus width, however, may be complicated by environmentally induced variability.

In conclusion, until we fully understand how to reliably estimate lost annuli and account for issues that we uncovered, either method would be problematic to use in stock assessment and management of spiny dogfish in the Northeast Pacific Ocean. Though it is important to continue efforts to improve techniques to account for missing annuli while using the second dorsal fin spine, ultimately, no statistical extrapolation can ever fully make up for the large number of ages that may be missing from heavily worn spines. Thus, it is essential to explore alternative methods to reliably estimate ages in spiny dogfish sharks. Bubley et al. (2012), for example, proposed a new method to estimate spiny dogfish ages from vertebrae, but using a histological staining technique, which helps make banding pattern on a vertebrae much more visible and easy to read. Bubley et al. (2012) applied this method to the dogfish shark in the North Atlantic Ocean *S. acanthias* and demonstrated higher precision of the age estimates than those made based on the second dorsal spine, as well as good fit, and realistic parameters of the growth curves obtained from these estimates. It is hoped that the Bubley et al. method, or another, may soon result in age estimates for North Pacific spiny dogfish *S. suckleyi* of sufficient quality so they could be used to inform stock assessments and management for this species.

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