Abstract—Ten growth models were fitted to age and growth data for spiny dogfish (*Squalus acanthias*) in the Gulf of Alaska. Previous studies of spiny dogfish growth have all fitted the t_0 formulation of the von Bertalanffy model without examination of alternative models. Among the alternatives, we present a new two-phase von Bertalanffy growth model formulation with a logistically scaled k parameter and which estimates L_0. A total of 1602 dogfish were aged from opportunistic collections with longline, rod and reel, set net, and trawling gear in the eastern and central Gulf of Alaska between 2004 and 2007. Ages were estimated from the median band count of three independent readings of the second dorsal spine plus the estimated number of worn bands for worn spines. Owing to a lack of small dogfish in the samples, lengths at age of small individuals were back-calculated from a subsample of 153 dogfish with unworn spines. The von Bertalanffy, two-parameter von Bertalanffy, two-phase von Bertalanffy, Gompertz, two-parameter Gompertz, and logistic models were fitted to length-at-age data for each sex separately, both with and without back-calculated lengths at age. The two-phase von Bertalanffy growth model produced the statistically best fit for both sexes of Gulf of Alaska spiny dogfish, resulting in $L_\infty=87.2$ and 102.5 cm and $k=0.106$ and 0.058 for males and females, respectively.

Age and growth of spiny dogfish (*Squalus acanthias*) in the Gulf of Alaska: analysis of alternative growth models

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The spiny dogfish (*Squalus acanthias*) is a small long-lived shark common among temperate coastal areas in the Atlantic and Pacific oceans (Compagno, 1984). This species has been the target of commercial fisheries over much of its range, in some cases for over a century (Ketchen, 1986). In some areas, severe declines in population abundance and stock structure have occurred (e.g., Rago et al., 1998). Many elasmobranchs, including spiny dogfish, are "equilibrium strategists" that are highly susceptible to overfishing because of their slow growth rates, low fecundity, and late maturation (King and McFarlane, 2003), all of which are directly related to recruitment and parental stock sizes (Holden, 1974; 1977). Off the west coast of North America, spiny dogfish were depleted by intense fisheries in the 1940s, owing to the quantity and quality of vitamin A in their livers (Ketchen, 1986); the fishery demand decreased by 1950 with the development of synthetic vitamin A (Ketchen et al., 1983). Since the 1970s, spiny dogfish have continued to be targeted by commercial fisheries in British Columbia and the state of Washington for human consumption.

Although not targeted, spiny dogfish is a common bycatch species in many fisheries in both state and federal waters off the coast of Alaska. In the Gulf of Alaska (GOA) spiny dogfish are taken in Pacific salmon (*Oncorhynchus* spp.) gillnet fisheries, sablefish (*Anoplopoma fimbria*) fisheries, Pacific halibut (*Hippoglossus stenolepis*) longline fisheries, and groundfish trawl fisheries (Boldt, 2003). Although an estimated average of 482.1 metric tons (t) of spiny dogfish was taken annually from 1997 to 2007 in observed fisheries (Tribuzio et al., 2008), the bycatch in state waters is unknown and the bycatch rates in federally managed fisheries are likely underestimated because of unobserved fisheries (e.g., the halibut individual fishing quota, IFQ). Nearly all of this unintended bycatch was and still is discarded at sea. Even though estimated catch is <1% of estimated spiny dogfish biomass (Courtney et al., 2006), the potential development of a commercial fishery demands further investigation

of the effect of total fishing mortality on biomass and an investigation of spiny dogfish life history characteristics in Alaska.

Biological reference points (e.g., B_{MSY}, $F_{35\%}$) are benchmarks against which stock abundance or fishing mortality rates can be compared to determine stock status. Most commonly used reference points are functions of stock productivity, such as growth, recruitment, and natural mortality (Bonfil, 2005); thus accurate estimates of age and growth are important. For instance, estimates of age and the growth coefficient (k) are critical for estimating natural mortality (M), where a lack of data prevent direct estimation of M, abundance, and appropriate harvest rates. In the GOA, biological reference points, such as those from age and growth models, have yet to be determined for spiny dogfish.

Extension of life history parameters from other regions to Alaska may be inappropriate because age and growth characteristics of spiny dogfish vary widely over its geographic range. For example, maximum age in the northwest Atlantic Ocean is 35–40 years (Nammack et al., 1985), but in the eastern North Pacific, spiny dogfish have been aged to over 80 years (Saunders and McFarlane, 1993). Growth characteristics also vary widely throughout the North Pacific and North Atlantic oceans (Ketchen, 1975; Nammack et al., 1985). Even within the North Pacific basin, biological parameters, such as k, can vary with latitude (Vega, 2006).

The selection of an appropriate growth model is important when estimating regionally specific parameters. Elasmobranch age and growth studies have generally focused on fitting length-at-age data to the von Bertalanffy (vB) growth equation, irrespective of goodness-of-fit or alternative growth models (Carlson and Baremore, 2005). Despite its common use, the vB growth equation may not be the best-fit growth model for all elasmobranch species. For example, the logistic model fitted best among four models tested for the spinner shark (*Carcharhinus brevipinna,* Carlson and Baremore, 2005), and a two-phase vB model fitted best among five models for the piked spurdog (*Squalus megalops*, Braccini et al., 2007). A model that is not the best descriptor of a species' growth could have compounding effects on demographic analyses, stock assessment, and fishery management.

Typical growth models involve parameters of asymptotic length (L_∞), k, and t_0 (Cailliet et al., 2006). The t_0 parameter is biologically difficult to interpret because it is not measurable and testable in wild animals (Beverton and Holt, 1957). This parameter is the age at which the animal is of zero length and is based on an assumption of a fixed growth curve from fertilization through life (Beverton and Holt, 1957). It is generally interpreted to represent the period of gestation in teleost fish species, but this assumption is violated for elasmobranchs (Driggers et al., 2004). For instance, when considering males and females separately, models will estimate different t_0 values. If t_0 is truly representative of gestation time, then it leads to the incorrect inference that male and female pups have different gestation periods. For these reasons, growth models that use size at birth (L_0) instead of t_0 may be more appropriate for elasmobranchs (Cailliet and Goldman, 2004).

The purpose of this study was to estimate best-fit growth models for male and female spiny dogfish in the GOA. Resultant growth equations provide critical parameters for a better understanding of spiny dogfish biology, estimation of biological reference points including indirect estimates of M, improved stock assessments, and development of sound fishery management plans for this species in waters off Alaska.

Materials and methods

Sample collection

Spiny dogfish were collected by targeted sampling cruises, state and federal assessment surveys, and opportunistic fishery bycatch samples between July 2004 and April 2007 across the GOA (Fig. 1, Table 1 (delete bold font after placing tables). All spiny dogfish were sexed and length was measured to the nearest centimeter (total length extended=TL_{ext}; total length natural=TL_{nat}; precaudal length=PCL; and fork length=FL; Tribuzio et al., 2009). Here, length measurements are reported as total length extended (TL_{ext}). The posterior dorsal spine was removed and stored frozen for laboratory analyses. In the laboratory, spines were cleaned by thawing, by boiling briefly, and the loose tissue was scraped free. Spines were allowed to dry overnight and then stored in individual paper envelopes for subsequent age reading.

Sampling bias was examined because we sampled with multiple gear types in different locations. To test for potential bias, a chi-squared (χ^2) test was conducted to test for statistically significant ($P<0.05$) differences in the mean length at age by sex for each gear (trawl, setnet, longline, rod and reel) and region (Cook Inlet, Prince William Sound, Yakutat Bay, and Gulf of Alaska). Statistically significant differences among different gears would provide evidence of sampling bias. However, statistically significant differences among different geographic areas would provide equivocal evidence of bias because the possibility of true underlying differences in size distributions by area could not be dismissed.

Age determinations

The posterior dorsal spines were read in the laboratory according to the methods of Ketchen (1975) and Beamish and McFarlane (1985). Each band pair (hereafter termed "band"), consisting of one dark and one light band, was counted as one year or annulus (Cailliet et al., 2006). Aging was conducted by two scientists at the Washington Department of Fish and Wildlife's age laboratory and by the lead author at the University of Alaska Fairbankans. Ease of age reading was categorized from 1 (easiest) to 3 (most difficult). Spines were photographed on a 1×1 mm grid to standardize measurements. All measurements were rounded to the nearest 0.01 mm by using Bersoft
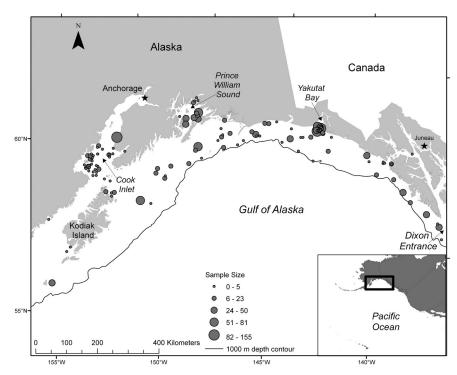
Figure 1

Locations where spiny dogfish (*Squalus acanthias*) were sampled in the Gulf of Alaska in 2004–07. The size of the circle is proportional to the number of spiny dogfish sampled at each location.

Table 1

Locations, gear types, and sample sizes for male and female spiny dogfish (*Squalus acanthias*) collected during 2004–07. "Sport" gear refers to hook-and-line fishing with rod and reel, "longline" refers to multiple hooks on a groundline, "trawl" denotes either bottom or pelagic trawls, and "set net" refers to a stationary floating gill net, generally anchored at one end to the shore.

Year	Area	Gear	Males (n)	Females (n)
2004	Yakutat Bay	Sport	21	91
2004	Gulf of Alaska (GOA)	Longline	52	85
2005	Southeast Alaska (SEAK)	Longline	1	13
2005	Yakutat Bay	Longline	11	23
2005	Yakutat Bay	Sport	0	15
2005	Cook Inlet	Sport	6	25
2005	Yakutat Bay	Longline	41	95
2005	GOA	Longline	112	204
2005	Cook Inlet	Sport	8	12
2005	Yakutat Bay	Sport	1	72
2005	Prince William Sound	Longline	27	69
2005	GOA	Trawl	83	125
2006	Kamishak Bay	Trawl	24	26
2006	Cook Inlet	Set net	50	90
2006	Copper River	Set net	9	5
2006	Yakutat Bay	Set net	4	57
2006	Icy Point (SEAK)	Trawl	0	1
2006	Prince William Sound	Longline	87	91
2006	Cherikoff Island (SW GOA)	Trawl	28	13
2007	Cherikoff Island (SW GOA)	Trawl	20	16

Image Measurement vers 5.0 software (Bersoft, Inc., http://bersoft.com). Measurements included spine base diameter (*SBD*), enamel base diameter (*EBD*), last readable point (*LRP*, also called the no-wear point); and, for nonworn spines, base length (*BL*), and spine total length (*TL*, Fig. 2) were also measured to the nearest 0.01 mm. Nonworn spines were those spines with a *LRP*<2.45 mm (McFarlane and King, 2009), which is the *EBD* at birth.

Aging bias and precision were evaluated for all three readers. Pair-wise age-bias plots were used to compare each reader against the other two (Campana et al., 1995) and a χ^2 test for symmetry was used to test for statistically significant systematic bias among the three readers (Hoenig et al., 1995). Readers were considered to be in agreement when ages were within 10% of each other rather than within some fixed 1- or 2-year age interval. For instance, if reader X counted 10 bands, then reader Y's count would have to have been between 9–11 bands to be in agreement, but if reader X counted 40 bands, then reader Y's count would have to be between 36–44 to be in agreement. We contend that the use of a percentage to define the interval size is more appropriate for this long-lived species. Finally, the coefficient of variation (CV) between readers was calculated according to Campana's methods (2001).

Spiny dogfish ages are not always equal to the number of counted bands for two reasons: 1) bands are deposited during embryonic development, and 2) because the external spines can become worn or can break off. This problem was addressed by a correction method for estimating the number of missing bands that was based on a regression of band counts on the *SBD* of unworn spines (Ketchen, 1975). This method was subsequently re-examined and accepted as the best available method for the original samples plus additional samples from the same geographic region (McFarlane and King, 2009).

Various regression approaches were compared to determine which method resulted in the best model for estimating the number of worn bands in spiny dogfish collected from the GOA, including: nonlinear least squares regression (NLS, Eq. 1), and ordinary least squares (OLS, Eq. 2):

$$Band\ count = b_0 EBD^{b_1} \qquad (1)$$

$$\ln(Band\ count) = \ln(b_0) + \ln(EBD)b_1, \qquad (2)$$

where b_0 and b_1 are estimated parameters (based on Ketchen 1975, McFarlane and King 2009). Also, we fitted parameters for Equations. 1 and 2 with weighted nonlinear least squares (WNLS) and weighted ordinary least squares (WOLS), where weights were applied to the residuals as follows: spines in readability cat-
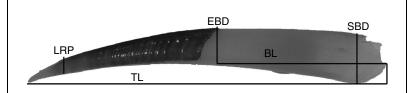

Figure 2

Measurements taken on spiny dogfish (*Squalus acanthias*) spines. Last readable point (LRP) is the point where the bands are no longer visible on the leading edge of the spine (upper edge in this picture). EBD = enamel base diameter, SBD = spine base diameter, BL = base length, and TL = spine total length, which only applies to spines that are unworn. All measurements were taken in millimeters.

egory 1 were given a weight of 1, those in category 2 were weighted by 0.5, and those in category 3 by 0.3. These values were chosen to discount the contribution of individual length at-age data points to the estimation process based on the degree of uncertainty in the age estimates for difficult-to-read spines. As an alternative to this weighting scheme, we explored the weighting process by using the inverse of the variance in assigned ages for each readability category. Ages of worn spines were then estimated by equating the *LRP* to the *EBD* in the best-fit model from Equations 1–4 and by adding the resultant number of bands to the median band count from the three readings and by subtracting two years (for bands deposited during gestation) to obtain the final estimated age of the animal (Ketchen, 1975). In the case of nonworn spines, age was estimated by the median band count minus two years. Data for males and females were combined for these worn band models.

Fitting of growth models

A total of 10 growth model variations were fitted separately to the length-at-age data for males and females (Table 2). The growth models included 1) the vB growth model for estimating t_0; 2) the two-parameter vB with fixed L_0; 3) the two-phase vB with L_0 (used in the present study); 4) the Gompertz; 5) the two-parameter Gompertz; and 6) the logistic. For comparison with previous studies L_0 is estimated for model 1 by setting $t=0$. An estimate of L_0 (i.e., the size at birth) for GOA spiny dogfish was not available; therefore model 2 was run with L_0 fixed at 26.2 cm (size at birth for spiny dogfish from British Columbia; Ketchen, 1972). Models 3 and 5 were run in three different ways: 1) L_0 was estimated by the model; 2) with L_0 set at the value estimated from model 1; and 3) with L_0 set at 26.2 cm. Model 3 is an adaptation of the two-phase vB model (Soriano et al., 1992). Standard fitting procedures with the two-phase model resulted in the A_t parameter from Soriano et al. (1992) changing for a brief time period and then returning to its original value. To correct this we reformulated the A_t parameter from Soriano et al. (1992); this treatment changes k, depending on the age of the dogfish, so that A_t would

Table 2
Growth models fitted to spiny dogfish (*Squalus acanthias*) length-at-age (L_t) data. Parameters are: asymptotic length (L_∞), the growth coefficient (k), length at birth (L_0), age at size zero (t_0), a phase change parameter (A_t) for the two-phase model, age at transition (t_h), magnitude of the maximum difference between model 1 and the two phase model (h), time increment from previous t value (δ), and the inflection point of the logistic curve (a).

Model number	Model name	Model equation	Reference
1	vB 1	$L_t = L_\infty\left(1 - e^{-k(t-t_0)}\right)$	von Bertalanffy (1938)
2	vB 2	$L_t = L_\infty - \left(L_\infty - L_0\right)e^{-kt}$	Fabens (1965)
3a–3c	Two-phase vB with L_0	$L_t = L_{t-\delta} + \left(L_\infty - L_{t-\delta}\right) * \left(1 - e^{-A_{t-\delta}k(t-t_{-\delta})}\right),$ $A_t = 1 - \dfrac{h}{1 + e^{slope(t_h - t)}}$	This study
4	Gompertz	$L_t = L_\infty e^{-e^{\left(-k(t-t_0)\right)}}$	Ricker (1975)
5a–5c	Two-parameter Gompertz	$L_t = L_0 e^{G\left(1-e^{-kt}\right)}, G = \ln\dfrac{L_\infty}{L_0}$	Mollet et al. (2002)
6	Logistic	$L_t = \dfrac{L_\infty}{1 + e^{-k(t-a)}}$	Ricker (1979)

follow a logistic pattern and remain in the second phase. Another problem we encountered fitting the two-phase model was that the typical differential form of the vB equation can result in a decrease in length at the transition between phases. To prevent this unlikely result the difference equation form of the vB equation (Gulland 1969) was used in this analysis.

Model parameters for equations describing the number of worn bands or growth were fitted by nonlinear least-squares regression or ordinary least-squares regression, and confidence intervals were estimated by a bootstrap procedure with 5000 replicates by using R statistical software (R, vers. 2.10.0, www.r-project.org). Confidence intervals (95%) for parameter estimates were based on the lower and upper 2.5th percentile of the bootstrap replications. Parameters were considered significantly different if the 95% confidence intervals did not overlap. To evaluate best model fit for the male and female datasets, Akaike information criteria (AIC) and model summary statistics were calculated (Burnham and Anderson, 2004).

Back-calculation methods

Owing to a paucity of specimens with *EBD*<3.5 mm, back-calculation methods were used to fill in the size range missing from samples. The spine diameter at each band along the spine (hereafter called "band diameters") was measured from a random subsample of 153 unworn spines for use in the estimation of worn bands (Eqs. 1–4); spiny dogfish with unworn spines tend to be smaller and younger than those with worn spines. We examined the Dahl-Lea, linear Dahl-Lea, and size at birth modified

Fraser-Lee back-calculation methods (Francis, 1990; Campana, 1990; Goldman et al., 2006). The Fraser-Lee method produced results that on an individual level could be quite unreasonable (large negative ages), but on average were more biologically reasonable than either of the Dahl-Lea methods. Further, growth model results with either of the Dahl-Lea methods were unreasonable (L_∞ of >150 cm TL_{ext}), therefore, we used the Fraser-Lee method for our data. Thus, the following equation was used to estimate back-calculated length-at-age data:

$$TL_i = TL_c + \frac{\left(EBD_i - EBD_c\right)\left(TL_c - TL_{birth}\right)}{EBD_c - EBD_{birth}}, \qquad (3)$$

where TL_i = the back calculated length;
TL_c = the length at capture;
TL_{birth} = the length at birth;
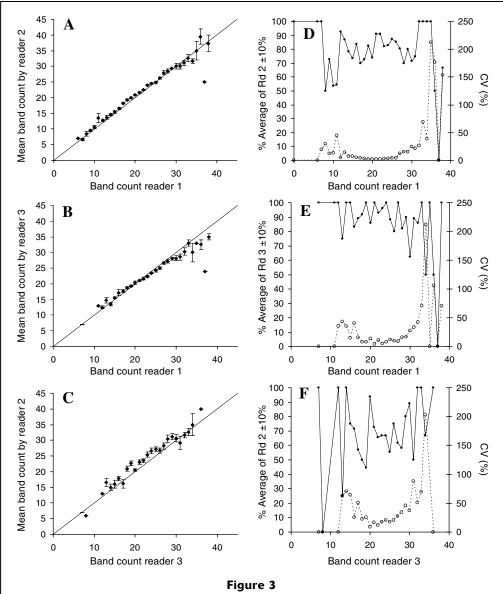EBD_i = the enamel base diameter at band *I*;
EBD_c = the enamel base diameter at capture; and
EBD_{birth} = the enamel base diameter at birth.

Results

Sample collection

A total of 1713 spiny dogfish were sampled over the four years of the study (585 males, 1128 females, Table 1) of which 537 male and 1062 female spines were usable. Lengths ranged from 56 to 99 cm TL_{ext} for males, and 56 to 123 cm TL_{ext} for females. The χ^2 test revealed no significant differences between the mean length at age

Figure 3

A comparison of age counts among readers. (**A**) Reader 2's mean band counts (*y*-axis) in relation to the band counts of reader 1; (**B**) Reader 3's mean band counts in relation to the band counts of reader 1; and (**C**) Reader 2's mean band counts in relation to the band counts of reader 3. Vertical lines are 95% confidence intervals and the diagonal line is the 1:1 relationship line. (**D**) Percent agreement and coefficient of variation for reader 2 (Rd 2) compared to reader 1. The percent agreement (±10%) is represented by the solid line and circles and the coefficient of variation (CV) by the dashed line and open circles. (**E**) Percent agreement and coefficient of variation of reader 3 (Rd 3) compared to reader 1; and (**F**) Percent agreement and coefficient of variation of reader 2 (Rd 2) compared to those of reader 3.

of any of the data groupings ($P>0.99$, $0.019<\chi^2<4.525$). Thus, we failed to find evidence of sampling bias or geographic differences in average size at age.

Age determinations

Sampled dogfish ranged in age from 8 to 50 years old. The χ^2 test and the age-bias plots indicated no signifi-

cant systematic bias between the three readers ($\chi^2=241$, 206, and 259 between readers 2 and 1, readers 2 and 3, and readers 3 and 1, respectively; all $P>0.05$; Fig. 3, A–C). The percent agreement between readers 2 and 1 (Fig. 3D) and readers 3 and 1 (Fig. 3E) was high for band counts less than 30 but was more variable or decreased for band counts greater than 30 (Fig. 3, D–F). For readers 2 and 3, the percent agreement was

Table 3

Summary of the parameters used in the worn-band estimation models and model fits for spiny dogfish (*Squalus acanthias*). The observed data are sample data, the band-diameter data were determined from a subsample of unworn spines where the diameter of each band was measured to simulate bound count at spine size for younger animals that were not sampled in this study. Regression models are ordinary least squares (OLS), weighted ordinary least squares (WOLS), nonlinear least squares (NLS) and weighted nonlinear least squares (WNLS). Estimated model parameters (95% confidence intervals in parentheses) and goodness-of-fit indicator AIC, the Akaike information criteria.

		Observed sample data $n=685$		Observed band-diameter data $n=3877$	
Model	Parameter	Estimate	AIC	Estimate	AIC
OLS	b_0	2.690 (1.952–3.708)	6.205	0.211 (0.199–0.223)	3.738
	b_1	1.135 (0.949–1.322)		2.867 (2.825–2.910)	
WOLS	b_0	2.471 (1.788–3.415)	6.219	0.212 (−0.201–0.224)	3.721
	b_1	1.179 (0.991–1.367)		2.856 (2.814–2.898)	
NLS	b_0	4.325 (3.400–5.444)	4.016	0.539 (0.487–0.594)	3.781
	b_1	0.955 (0.807–1.111)		2.241 (2.178–2.309)	
WNLS	b_0	4.009 (3.106–5.231)	4.018	0.528 (0.475–0.586)	3.763
	b_1	0.998 (0.826–1.164)		2.247 (2.180–2.318)	

more variable for band counts less than 20 (Fig. 3F). The CV between all three readers was generally low (<30%) for band counts less than 30, and there was a notable increase in the variability and CV for band counts greater than 30.

Spiny dogfish spines grow in a predictable pattern with age (Fig. 4). The brownish-black banded, enameled portion of the spine grows in length at a faster rate than the white base portion.

Inclusion of the back-calculated band diameter data dramatically changed the worn band estimation models (Fig. 5), and therefore further worn band estimations were made with both the observed and back-calculated band diameter data. There were no significant differences between the estimated worn-band model parameters, but the WOLS model had the lowest AIC value and therefore was chosen as the best-fit model (Table 3). Alternative fits to the WOLS and WLNS models, based on weightings by using the inverse variance in assigned ages for each readability category, yielded very similar parameter values and nominally poorer fits indicated by slightly larger AIC values (not shown). A high degree of natural variation resulted in wide 95% confidence intervals for all parameters. Moreover, parameter confidence intervals for the WOLS GOA model widely overlapped the parameter confidence intervals for the Hecate Strait and Strait of Georgia models (McFarlane and King, 2009). Although the parameters were not statistically significantly different, the GOA, Hecate Strait, and Strait of Georgia models appear to represent biologically meaningful differences in growth (Fig. 5). The Hecate Strait and Strait of Georgia models tend to overestimate the band count for larger spines and underestimate for smaller spines of spiny dogfish collected from the GOA.
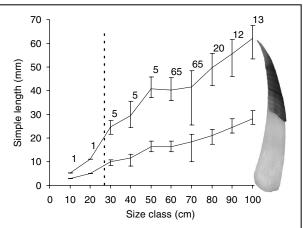

Figure 4

Relationship between mean second dorsal spine length and fish size determined from unworn spines from spiny dogfish (*Squalus acanthias*) collected in the Gulf of Alaska. The top line is spine total length (*TL*) and bottom line is base length (*BL*) in millimeters. Numbers above upper line represent the sample size for each 10-cm size class. Solid vertical lines represent 95% confidence intervals. The dashed vertical line represents the approximate size at birth (Ketchen, 1972).

Fitting of growth models

The two-phase vB models fitted the observed data best for males and females based on AIC values (Fig. 6, A and D, Tables 4 and 5). For males, the two-phase model, where L_0 was used from model 1 (model 3b), was the best fit and for females, it was the model where L_0 was estimated from model 1 (model 3b). Estimated (and 95%

confidence limits) asymptotic lengths (L_∞) were 87.2 cm (range 85.3–90.0 cm) and 102.5 cm (range 99.9–106.3 cm) and growth coefficients (*k*) were 0.106 (range 0.097–0.117) and 0.058 (range 0.052–0.063) for males and females, respectively. After including the back-calculated data and the mean back-calculated data, the two phase models were no longer the best fit for males. The best-fit model with inclusion of back-calculated data was model 2, and model 1 fitted best for the data including the mean back-calculated data. Similarly, for females the two-phase models were not the best-fit based on AIC values after the inclusion of back-calculated and mean back-calculated data: model 6 was the best fit with inclusion of back-calculated data, and model 5c (with L_0 from model 1) was the best fit for the data including the mean back-calculated data (Tables 4 and 5, Fig. 6, B, C, E, F).

Predicted length at age was similar for males and females for the observed data, up to about age 15, when a transition between growth phases occurred (Fig. 6). After the transition, females continued to grow at a faster rate and to larger sizes than males (Fig. 6, A and D). At the point of transition in the two-phase models growth increased for about five years before slowing, for both sexes.

Discussion

The model fits for all 10 examined growth models were similar and had very small differences in AIC, but the estimated parameters differed substantially; for example, the growth coefficient (*k*) was significantly different between some models and thus could impact estimates of natural mortality and subsequent demographic analyses. The values of *k* tended to fall into two groupings (in both data sets), and those models that estimated the higher *k* were also those that estimated lower estimates for L_∞. Interestingly, even with the significantly different estimates of *k*, these estimates were still at the lower range of reported growth rates for different types of shark species (Cailliet and Goldman, 2004).

Cailliet et al. (2006) recommended considering more than one form of evaluation of model performance and considering biological interpretations along with statistical fit when choosing the best model. Mean squared error and the correlation coefficient (r^2) were also calculated for each model, but determinations of best fit by the above criteria did not differ from those where AIC was used and therefore are not reported. For the observed data models 3a and 3b were the statistical best fit for males and females, respectively. However, the two-phase models tended to be unstable and would converge at different localized minima, depending on
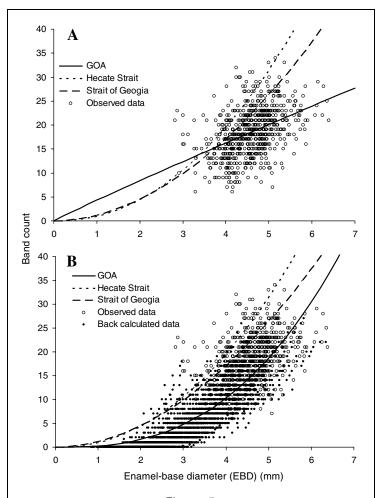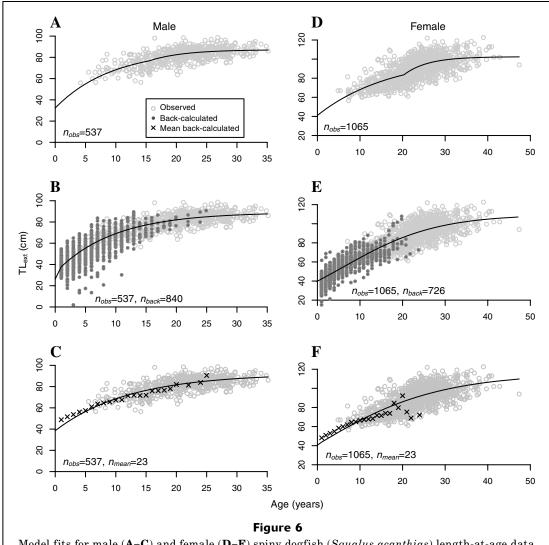

Figure 5

Relationship of band count to enamel-base diameter for spiny dogfish (*Squalus acanthias*) collected in the Gulf of Alaska (GOA) between 2004 and 2007. The best-fit model (weighted ordinary least squares [WOLS]) for (**A**) the observed data only and (**B**) the observed data with the band-diameter data; both sections A and B show the published best-fit relationships for spiny dogfish collected from Hecate Strait and the Strait of Georgia, British Columbia (McFarlane and King, 2009) for comparison.

the starting value. A further consideration for the two-phase models is that the growth curve indicates a period of rapid growth immediately following the age at transition.

The purpose of a two-phase model is to incorporate changes in energy allocation as animals grow: immature fish use surplus energy for growth, whereas mature fish use surplus energy for reproduction (Soriano et al., 1992). Thus, the rate of growth changes after maturation. In our case, the transition between the two growth phases occurred before the age at 50% maturity for both males and females The early age at transition and the period of rapid growth after transition indicate that for female spiny dogfish there is a "growth spurt" about 15 years before age at 50% maturity. For

Figure 6

Model fits for male (**A–C**) and female (**D–F**) spiny dogfish (*Squalus acanthias*) length-at-age data. (A and D) Best-fit growth models based on the observed sample data; (B and E) best-fit growth models based on the observed sample data and the back-calculated data; and (D and F) best-fit growth models based on the observed sample data and the mean back-calculated data. n_{obs} is the number of samples, n_{back} is the number of data points created through back calculation of the ages from band-diameter data, and n_{mean} is the number of mean back-calculated data points.

males, the pattern was similar, but occurred just before age at 50% maturity. This finding does not follow the theory behind the two-phase model and indicates that a two-phase model may not be most appropriate in this situation.

The two-phase vB model by Soriano et al. (1992) has been examined with data sets from many species of sharks to determine whether it is an adequate descriptor of shark growth (Araya and Cubillos, 2006). Whereas the two-phase model was better than the standard vB model in 8 of 11 species for females and 7 of 11 for males, the two-phase model did not perform better than the vB (model 1 here) for spiny dogfish. Because Araya and Cubillos (2006) included only one spiny dogfish population (Black Sea), which appears to have different

age and growth characteristics from those in the GOA, and only examined average length at age data (Avsar, 2001), we felt that it was worth while to investigate the two-phase family of models in this study. Braccini et al. (2007) found that the two-phase model was the best statistical fit for the piked spurdog, which is a species similar to spiny dogfish; however, the resultant models showed some of the same characteristic difficulties that we encountered. Those results also indicated a decrease in length after transition (Fig. 7, Braccini et al. 2007) and that the A_t parameter appears to change only briefly before returning to its original value. Braccini et al. did not address these issues as we have attempted here. A more comprehensive examination, which would include multiple data sets from different regions for

Table 4

Summary of male growth model results for spiny dogfish (*Squalus acanthias*). The "Observe data" were the actual age at length data from individual spines, the "With back-calculated data" were the observed data with the estimated back-calculated size-at-age data and the "With mean back-calculated data" were the observed data with the mean size-at-age from the back-calculated data. Estimated model parameters with 95% confidence intervals in parentheses and Akaike information criteria, AIC. Asymptotic length (L_∞) and size at birth (L_0) are in centimeters. The growth coefficient (k) and the theoretic age-at-size length zero (t_0) are not reported with units. In model 1, L_0 was solved for by setting $t_0=0$, this allowed for comparison with other studies.

Model number	Model equation	Parameter	Observed data n=537 Estimate (95% CI)	AIC	With back-calculated data n=1377 Estimate (95% CI)	AIC	With mean back-calculated data n=562 Estimate (95% CI)	AIC
1	$L_t = L_\infty\left(1-e^{-k(t-t_0)}\right)$	L_∞	88.3 (87.0–89.7)	4.545	94.5 (92.0–97.6)	4.476	92.1 (89.5–95.6)	4.436
		k	0.095 (0.083–0.107)		0.076 (0.068–0.085)		0.082 (0.065–0.099)	
		t_0	−4.8 (−6.5–−3.4)		−5.6 (−6.3–−4.9)		−6.6 (−9.4–−4.5)	
		Calculated L_0	32.3 (27.4–36.3)		32.7 (32.1–33.2)		38.4 (34.4–40.9)	
2	$L_0=26.2$ $L_t = L_\infty - (L_\infty - L_0)e^{-kt}$	L_∞	87.7 (86.6–88.8)	4.474	89.3 (87.8–90.9)	4.435	89.2 (87.9–90.6)	4.457
		k	0.105 (0.098–0.113)		0.104 (0.098–0.110)		0.109 (0.101–0.117)	
3a	$L_t = L_{t-\delta} + (L_\infty - L_{t-\delta})*\left(1-e^{-A_{t-\delta}k(t-t-\delta)}\right)$ $A_t = 1-\dfrac{h}{1+e^{slope(t_h-t)}}$	L_∞	87.6 (85.7–89.5)	5.58	89.3 (86.2–94.9)	4.570	87.5 (85.8–90.4)	4.504
		k	0.062 (0.034–0.085)		0.087 (0.074–0.098)		0.090 (0.072–0.104)	
		h	−2.0 (−5.8–−1.0)		−0.6 (−2.0–0)		−1.0 (−2.4–−0.3)	
		t_h	15.4 (13.5–17.6)		14.3 (10.9–18.1)		15.7 (13.4–17.5)	
		L_0	54.6 (46.0–63.1)		32.5 (31.0–34.0)		40.4 (34.3–46.7)	
3b	$L_0=$ from model 1	L_∞	87.2 (85.3–90.0)	4.472	89.5 (86.4–94.2)	4.565	87.1 (85.8–90.1)	4.507
		k	0.106 (0.097–0.117)		0.086 (0.076–0.094)		0.100 (0.087–0.108)	
		h	−0.7 (−2.8–−0.2)		−0.6 (−2.1–−0.0)		−2.3 (−6.5–−0.4)	
		t_h	15.4 (12.2–19.2)		14.3 (10.9–18.2)		20.0 (19.6–20.9)	
3c	$L_0=26.2$	L_∞	86.9 (85.1–88.8)	4.490	85.9 (83.9–89.1)	5.549	86.3 (85.1–90.0)	4.526
		k	0.116 (0.106–0.128)		0.114 (0.101–0.118)		0.121 (0.107–0.128)	
		h	−0.5 (−2.9–−0.1)		−1.3 (−6.2–−0.1)		−2.6 (−4.6–−0.1)	
		t_h	15.4 (12.0–19.7)		16.0 (13.3–19.3)		20.0 (14.7–20.3)	
4	$L_t = L_\infty e^{-e^{(-k(t-t_0))}}$	L_∞	87.5 (86.3–88.8)	4.559	90.6 (88.8–92.6)	4.477	90.9 (88.7–93.8)	4.458
		k	0.115 (0.100–0.132)		0.111 (0.102–0.120)		0.099 (0.081–0.119)	
		t_0	−1.1 (−2.7–−0.3)		−0.3 (−0.6–−0.0)		−2.5 (−4.5–−1.0)	
5a	$L_t = L_0 e^{G(1-e^{-kt})}$ $G = \ln\dfrac{L_\infty}{L_0}$	L_∞	87.8 (86.3–88.8)	4.557	90.6 (88.7–92.7)	4.479	90.9 (88.7–93.8)	4.458
		L_0	36.3 (30.6–41.4)		34.3 (33.0–35.6)		41.8 (36.7–46.5)	
5b	$L_0=26.2$	k	0.116 (0.100–0.132)	4.570	0.111 (0.102–0.121)	4.515	0.099 (0.082–0.119)	4.492
		L_∞	86.3 (85.4–87.2)		85.6 (84.5–86.7)		87.1 (86.1–88.1)	
5c	$L_0=$ from model 1	k	0.144 (0.136–0.152)	4.556	0.163 (0.156–0.170)	4.475	0.154 (0.145–0.163)	4.557
		L_∞	87.0 (86.0–87.9)		89.3 (87.9–90.8)		89.8 (88.4–91.5)	
6	$L_t = \dfrac{L_\infty}{1+e^{-k(t-a)}}$	k	0.126 (0.119–0.134)	4.571	0.121 (0.115–0.127)	4.499	0.111 (0.102–0.120)	4.475
		L_∞	87.1 (86.0–88.5)		88.5 (87.0–90.1)		90.0 (88.2–92.6)	
		k	0.130 (0.111–0.151)		0.146 (0.135–0.157)		0.116 (0.096–0.137)	
		a	1.2 (−0.4–2.6)		2.8 (2.5–3.1)		0.3 (−1.1–1.5)	

Table 5

Summary of results from the female growth models for spiny dogfish (*Squalus acanthias*). The "Observed data" were the actual age at length data from individual spines; the "With back-calculated data" were the observed data with the estimated back-calculated size-at-age data," and the "With mean back-calculated data" were the observed data with the mean size at age from the back-calculated data. Estimated model parameters with 95% confidence intervals in parentheses and Akaike information criteria, AIC. Asymptotic length (L_∞) and size at birth (L_0) are in centimeters. The growth coefficient (k) and the theoretic age-at-size length zero (t_0) are not reported with units. In model 1, L_0 was solved for by setting $t_0=0$, this allowed for comparison with other studies.

Model number	Model Equations	Parameter	Observed data n=1065			With back-calculated data n=1791			With mean back-calculated data n=1090		
			Estimate	(95% CI)	AIC	Estimate	(95% CI)	AIC	Estimate	(95% CI)	AIC
1	$L_t = L_\infty\left(1 - e^{-k(t-t_0)}\right)$	L_∞	121.4	(112.9–137.6)	5.677	128.4	(122.3–136.5)	5.365	128.8	(118.6–148.7)	5.317
		k	0.034	(0.023–0.045)		0.037	(0.032–0.043)		0.036	(0.024–0.047)	
		t_0	−12.1	(−17.9–8.2)		−8.9	(−9.9–8.0)		−10.5	(−15.0–7.2)	
		Calculated L_0	40.9	(38.1–42.5)		36.4	(33.2–39.7)		40.3	(35.9–42.7)	
2	$L_0=26.2$; $L_t = L_\infty - (L_\infty - L_0)e^{-kt}$	L_∞	108.9	(106.3–111.9)	5.668	108.0	(106.0–110.2)	5.364	114.2	(110.8–118.1)	5.314
		k	0.055	(0.051–0.059)		0.067	(0.063–0.071)		0.057	(0.052–0.062)	
3a	$L_t = L_{t-\delta} + (L_\infty - L_{t-\delta})\ast\left(1 - e^{-A_{t-\delta}k(t-t-\delta)}\right)$	L_∞	102.5	(99.9–106.2)	5.371	103.8	(100.9–107.8)	5.387	101.7	(99.4–104.9)	5.374
		k	0.053	(0.040–0.064)		0.057	(0.052–0.063)		0.057	(0.048–0.065)	
		h	−2.5	(−4.3–1.5)		−1.5	(−2.4–0.9)		−2.2	(−3.7–1.4)	
		t_h	20.3	(19.2–21.8)		19.4	(18.1–20.6)		20.0	(19.4–20.5)	
		L_0	45.8	(37.5–54.3)		35.6	(34.3–37.0)		42.2	(35.8–48.4)	
3b	$A_t = 1 - \dfrac{h}{1 + e^{slope(t_h - t)}}$; $L_0=$ from model 1	L_∞	102.5	(99.9–106.3)	5.371	103.8	(101.5–113.1)	5.387	100.76	(98.8–103.4)	5.374
		k	0.058	(0.052–0.063)		0.057	(0.046–0.060)		0.061	(0.056–0.065)	
		h	−2.1	(−3.7–1.2)		−1.7	(−2.5–0.4)		−2.8	(−3.9–1.8)	
		t_h	20.3	(19.2–21.8)		19.8	(15.3–20.6)		20.8	(20.5–20.9)	
3c	$L_0=26.2$	L_∞	101.8	(99.2–105.4)	5.389	98.5	(96.5–100.0)	5.395	100.2	(98.2–102.7)	5.390
		k	0.073	(0.066–0.078)		0.081	(0.075–0.083)		0.076	(0.070–0.080)	
		$h=a$	−1.4	(−2.9–0.7)		−3.0	(−5.1–1.5)		−2.0	(−3.1–1.1)	
		$t_h=P50$	20.3	(18.8–22.1)		21.3	(20.4–21.9)		20.8	(20.5–20.9)	
4	$L_t = L_\infty e^{\left(-e^{-k(t-t_0)}\right)}$	L_∞	115.7	(109.2–127.4)	5.683	115.7	(112.2–119.9)	5.355	119.5	(112.5–130.5)	5.314
		k	0.048	(0.036–0.060)		0.064	(0.059–0.069)		0.056	(0.043–0.068)	
		t_0	−1.1	(−2.7–0.4)		1.6	(1.2–2.1)		0.3	(−0.8–1.5)	
5a	$L_t = L_0 e^{G\left(1-e^{-kt}\right)}$; $G = \ln\dfrac{L_\infty}{L_0}$	L_∞	115.6	(109.3–127.4)	5.681	115.7	(112.2–119.8)	5.355	119.5	(112.7–130.5)	5.314
		L_0	45.0	(40.1–49.9)		38.2	(37.1–39.3)		43.1	(38.4–47.6)	
5b	$L_0=26.2$	L_∞	102.4	(101.0–104.0)	5.660	100.1	(98.8–101.3)	5.412	105.9	(103.8–108.0)	5.330
		k	0.090	(0.086–0.094)		0.115	(0.111–0.120)		0.096	(0.091–0.101)	
5c	$L_0=$ from model 1	L_∞	111.2	(108.1–114.8)	5.539	112.1	(109.7–114.8)	5.410	116.0	(112.2–120.4)	5.309
		k	0.060	(0.053–0.061)		0.071	(0.068–0.075)		0.062	(0.057–0.067)	
6	$L_t = \dfrac{L_\infty}{1 + e^{-k(t-a)}}$	L_∞	112.3	(106.9–120.9)	5.687	109.8	(107.2–112.7)	5.352	114.5	(109.3–122.0)	5.310
		k	0.062	(0.049–0.075)		0.091	(0.085–0.097)		0.075	(0.062–0.089)	
		a	5.1	(3.8–6.7)		6.3	(5.7–6.9)		5.7	(4.7–7.0)	

each species, and a complete sample of the size range may lead to a more conclusive determination as to which species exhibit two-phase growth.

Disregarding the two-phase models, the best-fit model was model 2 for males and model 5c for females. In this situation, given the lack of data and difficulties with the two-phase models, it may be more appropriate to select the best model not based on the AIC criteria alone, but to also consider the biological soundness of the models. Model 2 (males) and model 5c (females) are the statistical best fit of the more biologically reasonable models. Both of these best-fit models require L_0 as an input, not as an estimated parameter. The lack of data for spiny dogfish <50 cm TLext likely causes the models that estimate L_0 to have difficulty fitting the data and as a result estimate L_0 to be larger than would be expected.

In the majority of published studies on spiny dogfish age and growth the traditional von Bertalanffy model is used. To facilitate a broader comparison of our results with growth parameter estimates for other regions of the geographic distribution of spiny dogfish, we compared parameters estimated from model 1 (Table 4) with growth curves fitted by using the traditional vB formulation, as reported in published studies (Table 5, Fig. 7). Clear differences in spiny dogfish growth exist between the North Pacific and North Atlantic oceans. For instance, we found that male and female dogfish reach larger asymptotic sizes (87.2 and 112.2 cm TL_{ext}, respectively) in the GOA than off the northeastern United States (82.5 and 100.5 cm TL_{ext}, respectively; Nammack et al., 1985). Indeed, virtually all studies have found large differences in growth of spiny dogfish between the North Pacific and North Atlantic (Table 5, Fig. 7). Fish from the North Atlantic tend to grow more rapidly, achieve smaller asymptotic sizes, and have shorter life spans than those from the Pacific. Differences in growth also exist within the Pacific (Table 5, Fig. 7). For example, our GOA growth estimates are similar to those for spiny dog-
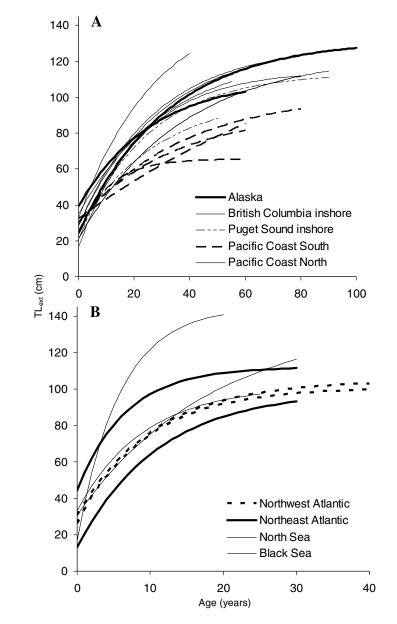

Figure 7

Comparison of published spiny dogfish (*Squalus acanthias*) female growth models from sources listed in Table 4. (**A**) Growth models published for Pacific Ocean spiny dogfish: "Alaska" includes the Gulf of Alaska (GOA) model from this study and a Prince William Sound (PWS) model (Vega, 2006); "British Columbia inshore" includes three models for dogfish sampled within the Strait of Georgia and Hecate Strait (Ketchen, 1975; Saunders and McFarlane, 1993); "Puget Sound inshore" covers models based on samples collected within the Puget Sound area south off British Columbia and east of the Washington coast (Vega, 2006); "Pacific Coast South" includes four models based on samples collected off Oregon and California (Vega, 2006); "Pacific Coast North" includes models based on samples collected off of Washington and the west coast of Vancouver Island (Ketchen, 1975; Jones and Geen, 1977; Vega, 2006); (**B**) The growth models from the Atlantic Ocean, North Sea. and Black Sea (Holden and Meadows, 1962; Sosinski 1978; Nammack et al., 1985; Fahy, 1989; Avsar, 2001; Henderson et al., 2002; Soldat [footnote 1 in Table 6]). Note the different *x*-axis scales.

Table 6

Summary of von Bertalanffy parameters (model 1) for growth models for female spiny dogfish (*Squalus acanthias*) from the North Pacific and North Atlantic oceans and the North and Black seas. Parameters are asymptotic length (L_∞) size at birth (L_0), growth coefficient (k), and the theoretic age-at-size length zero (t_0). Here, L_0 was solved for from the published parameter estimates for the purposes of comparison.

Location	L_∞	k	t_0	L_0	Reference
Alaska, Gulf of Alaska	121.4	0.034	−12.1	40.9	This study
Alaska, Prince William Sound	110.4	0.038	−11.6	39.4	Vega (2006)
British Columbia, Hecate Strait	125.1	0.031	−10.6	35.0	Ketchen (1975)
British Columbia, Strait of Georgia	129.1	0.034	−7.3	28.4	Ketchen (1975)
British Columbia, Strait of Georgia	114.9	0.044	−3.6	16.8	Saunders and McFarlane (1993)
British Columbia, offshore	128.5	0.036	−6.9	28.3	Jones and Geen (1977)
U.S., inshore (WA north)	113.5	0.04	−5.2	21.3	Vega (2006)
U.S., inshore (WA south)	100.4	0.036	−8.4	26.2	Vega (2006)
U.S., offshore (WA)	123.6	0.027	−6.9	21.0	Vega (2006)
U.S., offshore (WA)	152.9	0.036	−6.7	32.8	Ketchen (1975)
U.S., offshore (OR)	101.9	0.027	−12.7	29.6	Vega (2006)
U.S., offshore (OR and CA combined)	90.9	0.031	−13.0	30.2	Vega (2006)
U.S., offshore (CA north)	158.9	0.009	−25.3	32.4	Vega (2006)
U.S., offshore (CA south)	123.6	0.027	−6.9	21.0	Vega (2006)
Northwest Atlantic (U.S.)	100.5	0.106	−2.9	26.6	Nammack et al. (1985)
Northeast Atlantic (Ireland)	98.8	0.090	−1.6	13.3	Fahy (1989)
Northeast Atlantic (Ireland)	112.0	0.150	−3.4	44.7	Henderson et al. (2002)
Northwest Atlantic	104.5	0.095	−3.7	31.0	Soldat[1]
North Sea	137.1	0.054	−4.7	30.7	Sosinski 1978 (as cited in Avsar, 2001)
North Sea	101.4	0.110	−3.6	33.2	Holden and Meadows (1962)
Black Sea	145.0	0.170	−0.7	16.3	Avsar (2001)

[1] Soldat, V. T. 2002. Spiny dogfish (*Squalus acanthias* L.) of the northwest Atlantic Ocean (NWA). NAFO Sci. Counc. Res Doc 02/84, 33 p.

fish from offshore Washington State waters (Fig. 7) but greater than those caught in inshore Washington State waters (Puget Sound) and British Columbia (Ketchen, 1975; Jones and Geen, 1977; Saunders and McFarlane, 1993; Vega, 2006). The age and growth studies from British Columbia were conducted on spiny dogfish collected in inshore waters (Strait of Georgia and Hecate Strait); therefore the possibility cannot be ruled out that spiny dogfish from the British Columbia offshore region would have growth estimates similar to those of Washington offshore and GOA spiny dogfish. The vB growth model parameter estimates (L_∞ and k) for northern California spiny dogfish (defined as spiny dogfish between Point Conception to the Oregon border; Vega, 2006) were radically different from our results for the GOA, but the fits for California may have been adversely affected by small sample size.

The wide variability in length-at-age contributes to the lack of statistically significant differences among growth models and worn-band estimation models. This variability may be attributable to one or more of the following factors: measurement error in either length or age readings, sampling bias, true underlying variability in growth at age, and misidentification of worn and unworn spines. We considered the potential role of each of these factors.

Measurement error in the length measurements alone is insufficient to explain the relatively large variability in the size-at-age data. Aging errors may take two forms: imprecision and bias. We found no bias among the three readers tested, but imprecision of the band counts among readers could contribute to variability in the size-at-age data, especially for older ages. We used the median band count (from the three readers) to account for reduced precision because this measure of central tendency is less sensitive to outliers than the mean for small sample sizes (Dudewicz and Mishra, 1988). A more thorough analysis of the precision of age estimates for spiny dogfish in the Pacific Ocean revealed the overall coefficient of variation for aging estimates among four laboratories to be 19% (Rice et al., 2009). Systematic bias was found for two of the laboratories (one biased high, the other biased low) in relation to the other two, but relative bias did not always result in statistically different parameters estimated from vB growth curves (Rice et al., 2009).

Age validation is crucial for growth studies to assure that physical structures used for aging are correctly interpreted. For instance, a systematic aging error could result if the periodicity of band formation is not annual. Annual periodicity of band deposition on second dorsal spines was validated for spiny dogfish in British

Columbia (Beamish and McFarlane, 1985; McFarlane and Beamish, 1987). Moreover, radioactive carbon isotopes absorbed into spiny dogfish spines provided age estimates that agree with previous aging results for the British Columbia spiny dogfish (Campana et al., 2006) and verified that periodicity is annual, even at old ages (Campana, 2001). We assumed that this annual periodicity of band formation in spiny dogfish, which was confirmed for this species in British Columbia, also applies to fish from the GOA. Because spiny dogfish from British Columbia have different age characteristics (e.g., worn band curves, Fig. 5) from those of the GOA, it is possible that the pattern of band deposition may also differ.

Sampling bias was considered by examining potential differences in average size at age among gear type and location of capture. Because there were no significant differences among the average size at age with the different gear types used or the areas sampled, we do not believe that sampling bias was a significant factor affecting our results. However, the lack of significant differences in our study should not be misconstrued to rule out considerations of sampling bias in future spiny dogfish studies, because this species may school by size and sex (Nammack et al., 1985; Ketchen, 1986).

In the western North Atlantic Ocean commercial fisheries target the largest and oldest age classes (Rago et al., 1998). Thus, the size-frequency distributions determined from commercial catches may not be representative of the full size range of fish in the population. Moreover, depletion of large old fish from the population by heavy exploitation means that subsequent research surveys may not catch a representative sample of the full size and age ranges of the population. In the GOA, spiny dogfish are taken as bycatch in multiple fisheries. In some cases, dogfish bycatch is largely unaccounted for, owing to the lack of observers on small (<60-ft) vessels, such as those vessels with salmon gill nets, as well as some longline vessels targeting halibut and sablefish, resulting in an unknown level of total fishing mortality (Courtney et al., 2006). However, in the GOA, it is unlikely that the fishing mortality has truncated the size distribution of spiny dogfish because spiny dogfish are not targeted and recent (2006) estimates of spiny dogfish biomass are 80–100% of the estimated theoretical population carrying capacity (Rice, 2007). Therefore, it is unlikely that the fishery has created size-selective impacts that would lead to erroneous selection of the two-phase models as the best-fit models (Braccini et al., 2007).

One limitation of our size-frequency distributions is the absence of spiny dogfish smaller than 50 cm TL_{ext}. The lack of samples from smaller spiny dogfish is likely due to fishery-dependent opportunistic sampling which apparently occurs in areas devoid of juvenile spiny dogfish. Examination of NMFS spring and fall trawl surveys along the U.S. east coast revealed that in spring most juveniles were caught in water between 50 and 150 m deep (range: 7–390 m) in offshore waters from North Carolina to the eastern edge of Georges

Bank, whereas in fall most were caught between 25 and 75 m (range: 12–366 m) in various locations, such as on Georges Bank, Nantucket Shoals, and throughout the Gulf of Maine (McMillan and Morse, 1999). Spiny dogfish smaller than 50cm TL_{ext} have been surveyed in both Puget Sound, Washington (Tribuzio et al., 2009), and in the northern Strait of Georgia (McFarlane et al., 2006) by using bottom trawl gear. In this study, we made numerous unsuccessful attempts to capture juvenile dogfish smaller than 50 cm TL_{ext} in the GOA using sport and longline gear in Yakutat Bay, longline gear with small (10/0 circle) hooks in Southeast Alaska (K. Munk, personal commun.[1]), and commercial bottom trawls off Kodiak Island (J. Gauvin, personal commun.[2]).

A missing size group, such as small dogfish in our case, may cause growth models to overestimate t_0 or L_0, thus decreasing the k estimate. Further, this missing size group may have caused the age of transition, t_h, in the two-phase models to be underestimated. Also, the lack of small animals may have limited our ability to discriminate among competing growth models. We used band-diameter data and back-calculated lengths derived from unworn spines to attempt to address this data gap. The inclusion of the band-diameter data greatly improved the worn-band estimation models, but minimally changed the growth models. Few of the estimated growth model parameters based on the back-calculated and mean back-calculated data were significantly different from those estimated from the observed data alone.

Back-calculation methods are designed to be used when sample sizes are small or if sampling has not occurred each month (Cailliet and Goldman, 2004), but in this case it was the entire smaller end of the size range that was being estimated. With the modified Fraser-Lee size-at-birth method, we had to assume that average size at birth was known. We use 26.2 cm, which is based on data collected from spiny dogfish inside the Strait of Georgia, British Columbia (Ketchen 1972). Sizes at birth are reportedly similar for the species across the northern hemisphere, with ranges of 23–30 cm (Ketchen 1972, Tribuzio et al. 2009). We also assumed that 2.45 mm was the spine diameter at birth, based on studies of British Columbia spiny dogfish (McFarlane and King 2009). Because this is an average as well, it is likely that some spines were classified as "unworn" when they were actually "worn." Spines that are classified as "unworn" can lead to underestimating the age, and in the case of the back-calculation resulted in instances where 20 cm or more of growth was predicted in the first year. Back-calculations may not be appropriate for this species when dorsal fin spines are used as aging structures, but may work well if a structure such as vertebrae are used.

The relatively large variability in size at age of spiny dogfish in the GOA could also reflect true underlying variability in growth rates. Individuals experiencing different thermal and feeding histories are expected to have different growth characteristics. It is also conceivable that our samples represent collections of dogfish from multiple, mixed populations. For instance, 4 of 2940 recoveries (0.14%) of spiny dogfish tagged in British Columbia were recovered in Alaska (McFarlane and King, 2003). Because the movements of spiny dogfish from other areas to and from Alaska are unknown, the degree of mixing is uncertain. However, there is no evidence of genetic differentiation in the Northeast Pacific based on analyses of eight microsatellite loci from dogfish sampled from the Bering Sea, the Gulf of Alaska, Strait of Georgia, Puget Sound, and the coasts of Washington, Oregon, and California (Hauser, 2009). Mixtures of spiny dogfish from other areas with growth characteristics that are different from those of Alaska resident dogfish could contribute to the variability in size at age that we observed in the GOA. Nevertheless, the existence of a statistically significant difference in growth rates from different areas of the Northeast Pacific (Vega, 2006; Table 4 this document) indicates that mixing is incomplete.

Our findings have at least two important implications for management of the species. First, for estimation of stock productivity and biological reference points for spiny dogfish in the GOA, it is important to use growth curves that are fitted to size-at-age data from dogfish captured in the GOA. Although alternative growth model parameters were not statistically significantly different from one another in our study, the variation among predicted length may be of biological significance. For instance, the worn-band estimation curves for the GOA and British Columbia resulted in very different estimates of ages (Fig. 5); use of growth curves for British Columbia would result in estimated numbers of worn bands from dogfish spines in the GOA that would be biased low. For example, for a spiny dogfish with a 1.8-mm *EBD*, the GOA model would estimate an age of one year, whereas both of the British Columbia models would estimate an age of four years. A fish with a 6-mm *EBD* would be estimated to be 30 years old by the GOA model and 46 and 37 years old by the two British Columbia models. Such biases in growth estimates may lead to biases in estimates of biological reference points for fishery management.

Second, as in other portions of their range, the largest spiny dogfish are the oldest females. Because commercial fisheries for spiny dogfish select for the largest individuals, fishing mortality rates are disproportionately higher for this reproductive segment of the population. In the Northwest Atlantic Ocean, a sharp increase in landings during 1987–1993 led to a fivefold increase in fishing mortality rates on females from 0.016 to 0.26; and fishing mortality rates exceeding 0.10 on large (≥80-cm) females resulted in negative pup replacement, subsequently leading to stock decline (Rago et al., 1998). Thus, to sustain spiny dogfish in the GOA, fishery management plans should consider not only slow growth rates, low fecundity, and late maturation of this species (King and McFarlane, 2003), but also the potentially disproportionate number of removals of mature females from the stock by commercial fishing by estimating size- and sex-specific fishing mortality rates and biological reference points.

Future research should address the many uncertainties remaining about spiny dogfish biology and life history in Alaska. In particular, results from this study indicate several areas of research needed to improve our understanding of spiny dogfish age and growth. First, although demonstrated for fish captured off British Columbia (Beamish and McFarlane, 1985; McFarlane and Beamish, 1987; Campana et al., 2006), validation of annual band formation, as well as worn-band properties, for spiny dogfish collected from the GOA should be conducted to describe potential sources of bias in the age estimates for spiny dogfish at this northern portion of their range in the Pacific Ocean. Second, the collection of juvenile dogfish (<50 cm) is needed to provide more precise estimates of growth over their full life history, as well as to help identify statistically best-fit growth models. Third, tagging studies, such as those conducted in British Columbia (King and McFarlane, 2003), would help elucidate the degree to which dogfish in Alaska represent mixed stocks with different growth attributes; such tagging results would help to delineate stock boundaries essential for fishery management. Fourth, controlled experiments are necessary to fully examine the selectivity of various fishing gears for spiny dogfish by size and sex. This would be an important preliminary step toward gear standardization, if long-term sampling programs are envisioned for spiny dogfish. Finally, continued sampling of spiny dogfish over small regional scales is necessary to fully evaluate potential geographic differences in growth and resultant parameters (i.e., natural mortality) within the GOA, as well as to more broadly understand the life history of this species in this portion of its range. Although our study would not have been possible without the diversity of low-cost sampling opportunities afforded to us, including the valuable assistance of state and federal agencies and sport and commercial fishermen, further progress will be accelerated by a full-scale, directed field program, which would be more successful at providing an unbiased sample set of spiny dogfish in the waters off Alaska, and which would aid in efforts to build a more detailed stock assessment, and thus models of population dynamics.

Acknowledgments

Literature cited

Araya, M., and L. A. Cubillos
    2006.   Evidence of two-phase growth in elasmobranchs.   Environ. Biol. Fishes 77:293–300.
Avsar, D.
    2001.   Age, growth, reproduction and feeding of the spurdog (*Squalus acanthias* Linnaeus, 1758) in the southeastern Black Sea.   Estuar. Coast. Shelf Sci. 52:269–278.
Beamish, R. J., and G. A. McFarlane.
    1985.   Annulus development on the second dorsal spine of the spiny dogfish (*Squalus acanthias*) and its validity for age determination.   Can. J. Fish. Aquat. Sci. 42:1799–1805.
Beverton, R. J. H., and S. J. Holt.
    1957.   On the dynamics of exploited fish populations.   U.K Ministry of Agriculture and Fisheries, Fisheries Investigations 2, 533 p.
Boldt, J.
    2003.   Ecosystem considerations for 2004.   *In* Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands and Gulf of Alaska region, 335 p.   [Available from North Pacific Fishery Management Council, 605 W. 4th Ave., Suite 306, Anchorage, AK 99501.]
Bonfil, R.
    2005.   The purpose of stock assessment and the objectives of fisheries management.   *In* Management techniques for elasmobranch fisheries (J. A. Musick, and R. Bonfil, eds.), p. 6–14.   FAO Fisheries Tech. Paper 474.
Braccini, J. M., B. M. Gillanders, and T. I. Walker.
    2007.   Comparison of deterministic growth models fitted to length-at-age of the piked spurdog (*Squalus megalops*) in south-eastern Australia.   Mar. Freshw. Res. 58:24–33.
Burnham, K. P., and D. R. Anderson.
    2004.   Multimodel inference: understanding AIC and BIC in model selection.   Soc. Meth. Res. 33:261–304.
Cailliet, G. M., and K. J. Goldman.
    2004.   Age determination and validation in chondrichthyan fishes.   *In* The biology of sharks and their relatives (J. F. Carrier, J. A. Musick, and M. R. Heithaus, eds.), p. 399–447.   CRC Press, Boca Raton, FL.
Cailliet, G. M., W. D. Smith, H. F. Mollet, and K. J. Goldman.
    2006.   Age and growth studies of Chondrichthyan fishes: the need for consistency in terminology, verification, validation, and growth function fitting.   Environ. Biol. Fishes 77:211–228.

Campana, S. E.
    1990.   How reliable are growth back-calculations based on otoliths?   Can. J. Fish. Aquat. Sci. 47:2219–2227.
    2001.   Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods.   J. Fish Biol. 59:197–242.
Campana, S. E., C. Annand, and J. I. McMillan.
    1995.   Graphical and statistical methods for determining the consistency of age determinations.   Trans. Am. Fish. Soc. 124:131-138.
Campana, S., C. Jones, G. A. McFarlane, and S. Myklevoll.
    2006.   Bomb dating and age validation using the spines of spiny dogfish (*Squalus acanthias*).   Environ. Biol. Fishes 77:327–336.
Carlson, J. K., and I. E. Baremore.
    2005.   Growth dynamics of the spinner shark (*Carcharhinus brevipinna*) off the United States southeast and Gulf of Mexico coasts: a comparison of methods.   Fish. Bull. 103:280_291.
Compagno, L. J. V.
    1984.   Sharks of the world: an annotated and illustrated catalogue of shark species known to date, pt. 2: Carcharhiniformes, 675 p.   FAO Fish. Synop. 125 (vol. 4).   FAO, Rome.
Courtney, D., C. A. Tribuzio, K. J. Goldman, and J. Rice.
    2006.   GOA sharks.   *In* Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska for 2007, Appendix E, p. 481–561.   [Available from North Pacific Fishery Management Council, 605 W. 4th Ave., Suite 306, Anchorage, AK 99501.]
Driggers, W. B., J. K. Carlson, D. Oakley, G. Ulrich, B. Cullum, and J. M. Dean.
    2004.   Age and growth of the blacknose shark, *Carcharhinus acronotus*, in the western North Atlantic Ocean with comments on regional variation in growth.   Environ. Biol. Fishes 71:171–178.
Dudewicz, E. J., and S. A. Mishra.
    1988.   Modern mathematical statistics, 864 p.   John Wiley & Sons, Inc., New York, NY.
Fabens, A. J.
    1965.   Properties and fitting of the von Bertalanffy growth curve.   Growth 29:265–289.
Fahy, E.
    1989.   The spurdog *Squalus acanthias* (L) fishery in south west Ireland.   Irish Fish. Invest. Ser. B (Mar.) 32, 22 p.
Francis, R. I. C. C.
    1990.   Back-calculation of fish length: a critical review.   J. Fish Biol. 36:883–902.
Goldman, K. J., S. Branstetter, and J. A. Musick.
    2006.   A re-examination of the age and growth of sand tiger sharks, Carcharias Taurus, in the western North Atlantic: the importance of ageing protocols and use of multiple back-calculation techniques.   Environ. Biol. Fishes 77:241–252.
Gulland, J. A.
    1969.   Manual of methods for fish stock assessment: part 1, Fish population analysis.   FAO manuals in fisheries science, no. 4, 154 p.   FAO Rome.
Hauser, L.
    2009.   The molecular ecology of dogfish sharks *(Squalus acanthias)*.   *In* Biology and management of dogfish sharks (V. F. Gallucci, G. McFarlane, G. Bargmann, eds.), p. 229–252.   Am. Fish. Soc., Bethesda, MD.

Henderson, A. C., K. Flannery, and J. Dunne.
  2002.   Growth and reproduction in the spiny dogfish *Squalus acanthias* L. (Elasmobranchii: Squalidae), from the west coast of Ireland.   Sarsia 87:350–361.
Hoenig, J. M., M. J. Morgan, and C. A. Brown.
  1995.   Analyzing differences between two age determination methods by tests of symmetry.   Can. J. Fish. Aquat. Sci. 52:364–368.
Holden, M. J.
  1974.   Problems in the rational exploitation of elasmobranch populations and some suggested solutions.   *In* Sea fisheries research (E. H. Jones, ed.), p. 187–215. Logos, London.
  1977.   Elasmobranchs.   *In* Fish population dynamics (J. A. Gulland, ed.), p. 187–215. Wiley, London.
Holden, M. J., and P. S. Meadows.
  1962.   The structure of the spine of the spur dogfish (*Squalus acanthias* L.) and its use for age determination.   J. Mar. Biol. Assoc. U.K. 42:179–197.
Jones, B. C., and G. H. Geen.
  1977.   Age and growth of spiny dogfish (*Squalus acanthias*) in the Strait of Georgia, British Columbia.   Fish. Mar. Serv. Res. Dev., Tech. Rep. 699, 16 p.
Ketchen, K. S.
  1972.   Size at maturity, fecundity, and embryonic growth of the spiny dogfish (*Squalus acanthias*) in British Columbia waters.   J. Fish. Res. Board Can. 29:1717–1723.
  1975.   Age and growth of dogfish *Squalus acanthias* in British Columbia waters.   J. Fish. Res. Board Can. 32:43–59.
  1986.   The spiny dogfish (*Squalus acanthias*) in the northeast Pacific and a history of its utilization.   Can. Spec. Publ. Fish. Aquat. Sci. 88, 78 p.
Ketchen, K.S., N. Bourne, and T. H. Butler.
  1983.   History and present status of fisheries for marine fishes and invertebrates in the Strait of Georgia, British Columbia.   Can. J. Fish. Aquat. Sci. 48:1095–1119.
King, J. R., and G. A. McFarlane.
  2003.   Marine fish life history strategies: applications to fisheries management.   Fish. Manag. Ecol. 10:249–264.
McFarlane, G. A., and R. J. Beamish.
  1987.   Validation of the dorsal spine method of age determination for spiny dogfish.   *In* Age and growth in fish (R. C. Summerfelt, G. E. Hall, eds.), p. 287–300.   Iowa State Univ., Ames, IA.
McFarlane, G. A., and J. R. King.
  2006.   Migration patterns of spiny dogfish (*Squalus acanthias*) in the North Pacific Ocean.   Fish. Bull. 101:358–367.
  2009.   Re-evaluating the age determination of spiny dogfish *(Squalus acanthias)* using oxytetracycline and fish at liberty up to twenty years.   *In* Biology and management of dogfish sharks (V. F. Gallucci, G. McFarlane, G. Bargmann, eds.), p. 77–88.   Am. Fish. Soc., Bethesda, MD.
McFarlane, G. A., J. R. King, and V. R. Hodes.
  2006.   Biological results of the Strait of Georgia spiny dogfish (*Squalus acanthias*) longline survey October 18–31, 2005.   Can. Data Rep. Fish. Aquat. Sci. 1182, 24 p.
McMillan, D. G., and W. W. Morse.
  1999.   Essential fish habitat source document: Spiny dogfish, *Squalus acanthias,* life history and habitat characteristics.   NOAA Tech. Memo. NMFS-NE-150, 19 p.

Mollet, H. F., J. M. Ezcurra, and J. B. O'Sullivan.
  2002.   Captive biology of the pelagic stingray, *Dasyatis violacea* (Bonaparte, 1832).   Mar. Freshw. Res. 53:531–541.
Nammack, M. F., J. A. Musick, and J. A. Colvocoresses.
  1985.   Life history of spiny dogfish off the Northeastern United States.   Trans. Am. Fish. Soc. 114:367–376.
Rago, P. J., K. A. Sosebee, J. K. T. Brodziak, S. A. Murawski, and E. D. Anderson.
  1998.   Implications of recent increases in catches on the dynamics of Northwest Atlantic spiny dogfish (*Squalus acanthias*). Fish. Res. 39:165–181.
Rice, J.
  2007.   Population dynamics of spiny dogfish (*Squalus acanthias*) in the Gulf of Alaska with an emphasis on the analysis of bycatch data.   M.S. thesis, 109 p.   Univ. Washington, Seattle.
Rice, J., V. F. Gallucci, and G. H. Kruse.
  2009.   Evaluation of the precision of age estimates for spiny dogfish.   *In* Biology and management of dogfish sharks (V. F. Gallucci, G. McFarlane, G. Bargmann, eds.), p. 161–168.   Am. Fish. Soc,, Bethesda, MD.
Ricker, W. E.
  1975.   Computation and interpretation of biological statistics of fish populations.   Bull. Fish. Res. Board Can. 191:1–382.
  1979.   Growth rates and models.   *In* Fish physiology, vol. IX (W. S. Hoar, D. J. Randall, and J. R. Brett, eds.), p. 677–743.   Academic Press, New York.
Saunders, M. W., and G. A. McFarlane.
  1993.   Age and length at maturity of the female spiny dogfish, *Squalus acanthias*, in the Strait of Georgia, British Columbia, Canada.   Environ. Biol. Fishes 38:49–57.
Soriano, M., J. Moreau, J. M. Hoenig, and D. Pauly.
  1992.   New functions for the analysis of two-phase growth of juvenile and adult fishes, with application to Nile perch.   Trans. Am. Fish. Soc. 121:486–493.
Sosinski, J.
  1978.   Characteristics of the North Sea spurdog (*Squalus acanthias* L.) stock.   Fish. Biol. 8:9–22.
Tribuzio, C. A., V. F. Gallucci, G. Bargman.
  2009.   Reproductive biology and management implications for spiny dogfish (*Squalus acanthias*) in Puget Sound, WA.   *In* Biology and management of dogfish sharks (V. F. Gallucci, G. McFarlane, G. Bargmann, eds.), p. 181–194.   Am. Fish. Soc., Bethesda, MD.
Tribuzio, C. A., C. Rodgveller, J. Heifetz, D. Courtney, and K. J. Goldman.
  2008.   Assessment of the shark stocks in the Gulf of Alaska.   *In* Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska for 2009, chapter 18, p. 557–612.   [Available from North Pacific Fishery Management Council, 605 W. 4th Ave., Suite 306, Anchorage, AK 99501.]
Vega, N. M.
  2006.   Biogeography of the spiny dogfish, *Squalus acanthias*, over a latitudinal gradient in the Northeast Pacific.   M.S. thesis, 117 p.   Univ. Washington, Seattle, WA.
von Bertalanffy, L.
  1938.   A quantitative theory of organic growth (inquiries on growth laws II).   Human Biol. 10:181–213.