***Otolith independent growth estimates for Pristipomoides filamentosus in the Main Hawaiian Islands obtained from mark-recapture data***

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***Abstract***

*Pristipomoides filamentosus* is an important species in the Hawaiian archipelago, accounting for much of the catch for the commercial bottomfish fishery. In the late 1980s, a mark recapture study by the State of Hawaii’s Division of Aquatic Resources tagged 4,172 fish. Over the next decade 431 marked fish were recaptured by project personnel and fishermen. Using Bayesian and maximum likelihood approaches, growth parameters were estimated from the tagging data. Direct aging and length frequency data from previous growth studies were incorporated alongside tagging data to produce composite estimates of growth fit using maximum likelihood. Parameters estimated from tagging and composite data were compared to results of prior growth studies. Results highlight the presence of individual variability in in *P. filamentosus* due primarily to individual variability in the parameter . It is quite likely that previous reports of growth for the species in Hawaii, which have almost universally neglected this source of variability, have underestimated the and overestimated the parameters. These results have implications for fisheries management as growth is often an input for stock assessment models and used as a proxy for other life history traits.

***Introduction***

*Importance of Growth as a Life History Parameter*

An accurate picture of a species life history is fundamental to fisheries resource management. Growth is a key life history parameter and correlated with a number of other life history parameters including maturation length, maturation age, natural mortality rate, and maximum age (Thorson et al., 2017)*.* A comprehensive understanding of growth enables managers to predict future biomass and informing sustainable harvest goals. The von Bertalanffy growth function (VBGF) is a popular and widely used for characterizing the growth (Chen, Jackson & Harvey, 1992). In its standard form VBGF fits an asymptotic curve using the parameters and K to describe growth using the following equation (equation 1):

Where is the length of an individual at the time of sampling, *t,* and is a function of the Brody growth rate and the mean asymptotic length at which growth is zero. Quantified this way, *t,* is the individual’s age at the time of sampling while parameter represents the theoretical age at which fork length is zero if the growth curve were extrapolated to the x-intercept. (Patterson et al., 2001).

Direct aging, length frequency, and growth increment are three common approaches to estimating growth parameters. Length at age data is frequently used with the direct aging approach and include individual length measurements and age estimates, often derived from a morphological proxy (otoliths, scales, bones, spines). Accurately estimating individual ages are important to avoid biasing estimates of growth. In many tropical fishes, direct aging methods may not perform well due to weak environmental seasonality, poorly-defined growth phase, or when incremental growth of the proxy is episodic. Such errors tend to underestimate individual age leading to overestimation of , and can result in overexploitation of fishery resources (Campana, 2001). Radiometric methods can be also used to estimate or validate individual age from the composition ratios of morphometric proxies but use of these methods are relatively recent (Bennett, Boehlert & Turekian, 1982; Andrews et al., 2012)*.*

Length frequency approaches sample a cohort over time to estimate growth parameters. Using modal progression, growth is estimated by identifying unique cohorts from size frequency data and tracking the change in size over time. Length frequency approaches are useful for estimating growth in juvenile fish where relatively fast growth rates clearly segregate cohorts by length class but may not perform as well for older age groups where there is less variability in fork-length between cohorts. Parameter estimates may be further confounded by protracted spawning, inter-annual variability in spawning and recruitment, or differential selectivity of sampling gear (Pauly & Morgan, 1987). (Csirke, Caddy & Garcia in Pauly, and Morgan 1987).

Growth increment approaches where fish are captured, measured and tagged or marked with an unique identifier, and released for later recapture, remain one of the most reliable methods for determining growth in the field (Fabens, 1965). These methods use a re-parameterization of the von Bertalanffy growth function to estimate growth parameters independent of age estimates. Instead growth is characterized using the reported length of individuals during marking () and recapture (), and the associated time at liberty ( between the two events.

Early work with applying these methods to tagging data failed to accommodate individual variability from mean growth of the population, instead presuming that all individuals adhere to the same growth parameters and that the length of an individuals at the time of marking directly corresponded to their age. However, it is well known that individual variability in growth can often vary based on sex (Kirkwood and Somers, 1984), time of year (Appeldoorn, 1987), food availability (Kerrigan, 1994), the temperature (Green & Fisher, 2004), oxygen levels (Pichavant Person-le-Ruyet, J., Le Bayon, N., Severe, A., Le Roux, A., Boeuf, G., 2001), genetic factors (Devlin et al., 2001), etc. Tagging, in and of itself, may affect a fish’s growth (Laurs and Wetherall, 1981). Failure to account for individual variability can introduce severe bias during parameter estimation (Eveson, et al., 2007; Zhang, et al., 2009). Early approaches to estimating growth parameters using tagging data were incompatible with those from direct aging studies because tagging methods model growth as a function of size rather than age (Sainsbury, 1980; Francis, 1988a).

Analytical and statistical advances to Fabens’ method have been developed to address these shortcomings. A number of structural modifications to the form of von Bertalanffy’s growth function have been proposed to account for additional sources of variability and permit parameter comparisons across models fit with different data types. A common model form introduces an additional parameter, to explicitly account for uncertainty surrounding the age of individuals at the time of tagging for the purpose of reducing bias and accommodating modest measurement errors (Equation 3) (James, 1991; Palmer, Phillips & Smith, 1991; Wang, Thomas & Somers, 1995; Laslett, Eveson & Polacheck, 2002; Zhang, Lessard & Campbell, 2009).

By treating as a random variable, tagging data is fit to growth curves using age, permitting comparison between tagging and direct aging methods (Eveson, Laslett & Polacheck, 2004). Alternative fitting methods may also reduce bias when estimating growth parameters (Francis, 1988b; Maller & Deboer, 1988; Wang, Thomas & Somers, 1995; Eveson, Polacheck & Laslett, 2007; Zhang, Lessard & Campbell, 2009). Maximum likelihood and Bayesian fitting approaches model growth at the population level from distributions of growth parameters at the individual level (Francis, 1988b; Kimura, Shimada & Lowe, 1993; Wang, Thomas & Somers, 1995; Zhang, Lessard & Campbell, 2009). The flexibility of Bayesian approaches allows K and L∞ to be sampled independently in this manner and can account for prior information while estimating parameters, while maximum likelihood models typically treat K as a fixed effect (Wang, Thomas & Somers, 1995; Laslett, Eveson & Polacheck, 2002; Zhang, Lessard & Campbell, 2009). Advances in maximum likelihood models allow for the estimation of a single set of growth parameters integrating tagging, direct age, and length frequency data sources (Eveson, Laslett & Polacheck, 2004).

*Fishery Background*

*Pristipomoides filamentosus* is a species of long lived deep water snapper distributed throughout the tropical Pacific and Indian Oceans from east Africa to Hawaii and Tahiti, southern Japan to Northern Australia (Allen, 1985; Andrews et al., 2012). In Hawaii, the speciesis known by the common name opakapaka and constitutes a significant fraction of the commercial and recreational fishery harvest [Kimberlee Harding DLNR/PIFSC-JIMAR Report Email from Uncle Roy (RNVFISHING), Sundberg and UnderKoffler, 2011)]. Due to its economic and cultural significance, a number of studies have expended a great amount of effort to understand various aspects of the life history of this species.

Growth parameters for opakapaka have been estimated a number of times, both in Hawaii and elsewhere (Table 1). Prior growth estimates for opakapaka have been obtained primarily from direct aging methods using counts of otolith growth increments (Ralston & Miyamoto, 1983; Uchiyama & Tagami, 1984; Radtke, 1987; Demartini, Landgraf & Ralston, 1994) and/or integration of otolith increments (Ralston & Williams, 1988) to estimate individual age. However, age estimates obtained using bomb radiocarbon dating of otoliths obtained from 33 individuals from the North Western Hawaiian Islands indicated that individual longevity could exceed 45 years, greater than twice that previously estimated, suggesting that otolith growth in mature individuals can be episodic and that previous reports of fast growth rates and short lifespans for the species are the result of biased age estimates (Andrews et al., 2012). Growth parameters have also been estimated using length frequency of juvenile cohorts sampled in a known nursery, however this analysis used the length of the largest individual from direct aging work as a fixed value of to describe mean growth in the population (Moffitt & Parrish, 1996). In each of these studies, individual variability was not a considered. A recent review of an ongoing cooperative tagging study in the Hawaiian Archipelago used the methods of Gulland and Holt (1959) and Francis (1988) to fit growth parameters for Opakapaka. However, parameter estimates reported from this work differ significantly from one another and from prior growth studies (O’Malley, 2015). These discrepancies may stem from the limited size range of recaptured individuals.

*Objective*

In this analysis, Bayesian and maximum likelihood fitting approaches are applied to mark-recapture data collected in the Main Hawaii islands to estimate von Bertalanffy growth parameters for *Pristipomoides filamentosus*. A series of ensemble models incorporating direct age and length frequency data previously reported are then fit using maximum likelihood to produce composite sets of growth parameter estimates integrating all three data sources. The predictive capacity of growth parameters estimated from tagging and composite approaches are compared to estimates for the species previously estimated for the region to determine which models most accurately predict observed growth. This study differs from previous work as it quantifies growth from a previously unreported data set, with data spanning a range of size classes and an adult sample size over three times larger than those previously published. Additionally, data previously used to estimate growth in other studies have been incorporated to estimate the single set of parameters best describing growth from direct age, length frequency, and mark recapture data, while accounting for the effects of individual variability.

***Methods***

*Marking and Recapture*

Tagging data used in this study was obtained by biologists from Hawaii’s Division of Aquatic Resources (DAR) within the state’s Department of Land and Natural Resources (DLNR). Between 1989 and 1994, a mark-recapture program targeting *P. filamentosus* known as the Opakapaka Tagging Program (OTP) was administered by staff biologist Henry Okamoto. Operating from fishing vessels contracted out of Honolulu Harbor. OTPtagged 4,179 juvenile and adult fish in the Main Hawaiian Islands.

Fish were caught with hook-and-line fishing gear and hauled to the surface at a rate of 2-5 feet per second. Prior to tagging, each fish was placed in a holding container with aerated seawater for observation. If the stomach was inverted and full of gas, it was punctured using a small sharp instrument (e.g., scalpel, hypodermic needle, fish hook). A few scales were carefully removed and a small (~1 cm) incision was made near the fish’s anal opening to assist in expelling gas from the body cavity. Fish were observed in the holding container to ascertain survival likelihood and those appearing lively and upright were deemed suitable candidates for tagging. These fish were surgically implanted with a uniquely identifiable internal anchor tag with a monofilament streamer protruding from the incision in the peritoneal cavity. Each fish’s fork length was measured to the nearest 1/4 inch before being returned to sea headfirst with enough downward momentum to assist in counteracting buoyancy caused by any residual gas.

In the intervening years, 487 recaptures were recorded from 431 unique individuals for a recapture rate of 10.3%. Individuals recaptured by Okamoto and his team were outfitted with an additional tag following similar procedures during initial capture. For each individual, the location of capture (DAR statistical reporting grid), length at capture was recorded, along with the date of each recapture. Local commercial and recreational fishers were made aware of the program through fliers distributed at the local fish markets, to fish dealers, at fishing supply outlets, and posted at small boat harbors. Fishers were incentivized to report the location and depth tagged fish were landed with a $10 reward for the fork length and the date of recapture. Recaptures of marked opakapaka were reported up to a decade after tagging with the most recent fish reported in October of 2003 (Okamoto, 1993; Kobayashi, Okamoto & Oishi, 2008).

*Tagging Data*

The data collected by OTP was entered into an Excel spreadsheet with subsequent analysis performed in R (R Core Team, 2014) and the Bayesian statistical software WinBUGS (Spiegelhalter et al., 2003). Fish in the dataset that were not the of species of interest, for which no recapture was reported, or for which no tag identification number was recorded were removed from the data set. Fork lengths for the remaining individuals recorded at marking and recapture were linearly transformed from inches to centimeters prior to model fitting. The growth () and time at liberty (), were calculated from the data for each individual. If an individual was recaptured on more than one occasion, and were calculated between the first marking event and the last recapture so as to not invalidate assumptions of independence. Fish with less than 60 days were excluded from the dataset. This process yielded records of 384 fish for analysis.

*Direct Age and Length Frequency Data*

Datasets previously used to estimate growth for opakapakasampled from the Main and Northwestern Hawaiian Islands, across a range of sizes, were used to produce a parameter estimates in composite growth models. Direct ageing data consisted of three previously reported data sets incorporating ages estimated by analytical integration of the width of otolith increments (Ralston and Miyamoto, 1983, n = 65), counts of otolith micro increments (Demartini et al., 2014, n = 35), and through comparison of bomb radiocarbon derived C14:C12 ratios in otoliths to a standard reference obtained from hermatypic coral cores collected in the Main and Northwestern Hawaiian Islands (Andrews et al., 2012, n = 33).

*Parameter Estimation from Tagging Data*

Growth parameters were estimated for the opakapakatagging data following the Bayesian methodology of Zhang et al. (2009) and maximum likelihood methodology of Laslett et al. (2002) respectively.

*Bayesian Approach*

This approach uses a Fabens version of the von Bertalanffy growth curve but allows the parameters to vary among individuals. Hence the length upon recapture is expressed as:

This is parameterized such that is the length of individual i for the jth recapture, is the time-at-liberty for individual i for the jth recapture, is the relative age of individual i at tagging (age minus ), and and are the von Bertalanffy growth parameters for individual i. These Individual parameters were drawn from Gaussian distributions defining the population mean values for and . Uninformative priors were used for all input parameters, using Gaussian, gamma, beta, and uniform distributions following the approach of Zhang et al. (2009). The WinBUGS code for performing this analysis is listed in Appendix 1.

The model which allowed both the K parameter and parameter to vary across individuals as described above is henceforth referred to as Model 1. Three additional models were run in modified versions of the WinBUGS code. Model 2 uses a fixed parameter while allowing the parameter to vary across individuals. Model 3 uses a fixed parameter while allowing the K parameter to vary across individuals. Lastly, Model 4 uses both a fixed parameter and a fixed parameter. The term “fixed” in this context does not imply a user-specified constant value, but instead refers to the value that is estimated by the Bayesian modeling approach from a single distribution used to represent the mean growth process across all individuals, hence “fixed”. Model 4 would a-priori be most similar to the Fabens approach, with both fixed K and , but with the added feature of estimating ages at initial tagging within the Bayesian framework, an important methodological improvement (Wang, Thomas & Somers, 1995). Model 1 is the presumptive best estimate for opakapaka von Bertalanffy growth curve parameters, since it would allow the most flexible incorporation of individual variability in the parameter estimation process.

For each Bayesian hierarchical model run, the first 10,000 samples from the posterior distribution were treated as burn-in and discarded from the Monte Carlo simulation. Every 50th sample from the following 500,000 samples (number kept=10,000) was tabulated into the posterior distributions to reduce potential autocorrelation between sequential values or strings of values. The mean and values from the 10,000 kept samples were used as metrics of population mean values. Median values deviated from mean values by less than one half of 1 percent (Appendix 2), indicative of symmetrical distributions easily characterized by any descriptor of value tendency (i.e., mean, median, or mode). The results from the Fabens (1965) approach using Solver described above provided estimates of and (Table 1), which were used as initial starting points in the Bayesian hierarchical approach. Two additional chains were run starting with initial values 50% lower and 100% higher than the initial estimates which resulted in nearly identical solutions as shown in Appendix 2. Convergence was also ascertained by examination of the Gelman-Rubin statistic (Gelman & Rubin, 1992). The comparisons of Models 1-4 were accomplished by examining the coefficients of variation of the von Bertalanffy growth parameters and for each of the Models 1-4. If the coefficient of variation for the parameter was relatively stable whether the parameter was allowed to be variable across individuals or fixed for the population, then it might be inferred that treating this parameter on an individual basis is not warranted. If the coefficient of variation for the parameter increased when the parameter distribution was fixed for the entire population, then it might be inferred that treating this parameter on an individual basis is necessary.

*Maximum Likelihood Approach*

Model 5 was fit using the maximum likelihood approach of Laslett, Everson, & Polacheck (2002) using Equation 5.

This method derives growth parameters from joint distribution of an individual’s length at tagging and recapture to estimate growth parameters. This approach is most similar to model 2 in that individual asymptotic length, , is treated as a random normal effect with a mean and standard deviation , allowing for individual deviations from the population mean. While is treated as a fixed unknown parameter. The relative age at tagging, , is also treated random effect with a distribution composed of the age at tagging of each individual, . The distribution of is assumed to be lognormal with mean and standard deviation . Rather than using length increments, a bivariate normal joint distribution describing the lengths recorded at marking and recapture are used to estimate growth (See Laslett et al (2002) for the full method for deriving individual joint distributions). An unconditional joint density is then derived for each individual by integrating the joint distribution with respect to (E6).

Growth parameter estimates are estimated through maximization of the log-likelihood function obtained by summing the unconditional joint density of each (E7).

Confidence intervals for each parameter estimated were constructed from the parameter distribution of 10,000 successful bootstrap iterations. For each iteration, a bootstrapped data set with an equal number of observations was constructed from the original tagging data with replacement and the growth model refit to producing a new parameter set. The distribution of ach bootstrapped parameter was then used to calculate median values and two-sided 95% confidence intervals.

*Estimation of Ensemble Growth Parameters*

Opakapaka have been the focus of a several growth studies using a variety of methodologies to estimate growth parameters from a number of different data. These data sources can potentially refine growth estimates when combined in an ensemble model approach. A modified form of the integrated method for estimating growth parameters proposed by Eveson, Laslett, Polachek (2004) to incorporate direct aging and length frequency data with tagging data to estimate a single set of growth parameters that best described observed growth.

Length frequency data consisted of the size distribution of juvenile opakapaka sampled during 13 months between October 1989 and February 1991 reported by Moffitt and Parrish (1996). The reported fork length of captured fish was binned in 1 cm increments and presented in 13 histograms corresponding to each month of sampling. The number of fish of a given fork length captured during each moth of sampling was determined by overlaying a series of evenly spaced horizontal lines across the Y-axis of each histogram. Each increment corresponding to the height of one additional fish. The reconstructed data consisted of counts individual fish binned caught during each month of sampling to the nearest 1 cm. As reported, from October to February, catch distributions represent 1 and 2 year cohorts while only the 1 year cohorts were present from March to September (Moffitt & Parrish, 1996). Mean age of each cohort was estimated for each month from the sampling month and month of peak sampling, reported to be July(Luers, Demartini & B, 2017), resulting in age estimates ranging between 3 and 19 months. Using this method to extrapolate monthly length frequency data resulted in a total count of 1,048 individuals while in the original manuscript the authors reported capture and measurement of 1,047 individuals.

The reconstructed length frequency data was incorporated into the composite model using the two-step method described by Laslett et al 2004. During the first step, a Gaussian mixture model is fit using maximum likelihood and used to decompose the distribution of fork lengths from individuals sampled during discrete time periods for each cohort present in the data. This was accomplished using the normalmixEM function from the mixtools package in R (Benaglia et al., 2009) by constraining the mean of each distribution to its mode. A bimodal Gaussian mixture model was fit during the months of October-Feb, as two cohorts were reported present in the data. For the remaining sampling months, while a single cohort was observed the remainder of the year. The estimated mean fork length, and standard error, , of each cohort during each sampling period was then used to estimate growth parameters using E8.

With this model, and reflect the fishing year, month, and age cohort, respectively. The estimated age of each cohort during a sampling period is denoted by . This age is the difference in years between midpoint of the sampling period and the average day of birth for the cohort, estimated from the spawning period of the mature parent population, and, for simplicity, assumed to be free from error. Sampling error is described using a normal distribution, and residual model error is described with by the term . In contrast to tagging and direct aging components, there is a dearth of information available to estimate the components of asymptotic length, using length frequency methods and so this term is modeled as fixed effect, , rather than a random effect. The rationale for these decisions is discussed extensively in Eveson et al. 2004. From this, the expected mode fork length of each cohort, and associated variability during each sampling period was calculated by equations 9 and 10. The observed and predicted mode and variability were used to construct the negative log likelihood function (E11).

Four sources of direct aging data were used to fit our ensemble models. Ages for the first set of fish were estimated from analytical integration of otolith increment widths (Ralston & Miyamoto 1989). The second dataset consisted of juvenile fish aged using the total count of microincrements visible in sectioned otoliths (Demartini, Landgraf & Ralston, 1994). The third and fourth direct aging data sets consisted of fish whose age was determined from the radio-carbon signature present in each otolith and the pooled lead-radium ratio of fish pooled by size class (Andrews et al., 2012).

The method for estimating growth parameters from direct aging data components is described in detail in Eveson et al. 2004. Briefly, data is modeled using the familiar VBGF model described by equation E12.

Expected length for each individual and the variance of the measurement error is described by equations E13 and E14.

Where denotes the length of the fish*,* at age and is a fixed parameter, analogous to that represents the theoretical time at which the average fish has a length of 0. As with the model for tagging data, is treated as a random effect, normally distributed around with a standard deviation , and assumed to vary between individuals. is similarly random and is the individual measurement error drawn from the population distribution . Equation 15 describes the log-likelihood function derived from these equations.

An appropriate likelihood function was defined for each data source and used to construct an overall objective likelihood function (E16).

The objective function was the sum of the negative log-likelihood function for each data source, with its own scaling constant, *.* Two approaches used to define the scaling constant were used. The first equally weight each data source allowing each data source equal influence on the resulting parameter estimates. This was achieved by selecting a for each data source equal to the inverse of the number of observations for the data. The second weighted each data source relative to the number of observations of that particular data set (). A single set of growth parameters best describing the data was then obtained by minimizing the resulting objective functions using mle2 function in R (Bolker & Team, 2017).

Two thirds of the tagging data (n = 258) were randomly selected and used to train the models while the remaining third (n = 129) was reserved for evaluating each model’s predictive ability. In total, 7 models were fit incorporating six different sources of data of three data types. One model (Model 6) was fit using only the training tagging data. Models 7-12 differed from one another in the treatment of coefficients, whether direct aging data sources were assigned their own log-likelihood function or if these data sources were pooled, and if direct aging data from analytical integration of otolith increment widths were to be included (Table 2).

*Comparing model performance*

Models 6-12 were evaluated to determine which combination of weighting, data pooling, and data sources produced and parameter estimates best predicts observed growth. The performance of each model was evaluated using its respective and parameter estimates to predict length at recapture for the validation dataset using Equation 2. The variance (between the predicted (and observed (length of each fish recapture (E17) was used as a metric to compare each model’s performance, with smaller variance indicative of greater predictive ability.

The predictive performance of existing growth parameters previously reported (table 1) was similarly evaluated to one another and models 6-12 by comparing their respective variances.

Finally, the methods used to fit the ensemble model best predicting observed growth were used to fit entire data set and two-sided 95% confidence intervals estimated for each parameter from 10,000 bootstrap iterations. As with tagging data, the procedure for resampling direct aging data was straightforward and involved random sampling with replacement from the dataset to construct pseudo data sets with an equal number of observations as the original data. Bootstrapping length frequency data was slightly more complicated with each study period in the pseudo data resampled from the corresponding period of the extrapolated study data. Additionally, each study period in the pseudo dataset contained the same number of observations as in corresponding study period the original study data.

***Results***

*Marking and Recapture*

Of the 4,172 opakapaka tagged 431 individuals were recaptured at least once (10.5%). Mortality of fish upon release appeared to be generally low, facilitated by the strong tagging selectivity for healthy fish in good condition. Some immediate mortality was observed due to sharks and cetaceans or capture stress (4 individuals). Long-term mortality was thought to be relatively low based upon the high rates of tag return spanning many years. Hydra (small cnidarian polyps) biofouling of the tags was observed for some individuals with large times at liberty, with some lesions apparent around the opening where the tag exited the body cavity. This was not thought to be a serious health issue since the fish appeared to be feeding and swimming normally.

During initial capture, the fork length of all individuals ranged in size between 19.05 and 52.93 cm with a mean (+/- se) fork length of 32.82 cm (+/- 0.24) and ranged from 19.1 cm and 52.8 cm with a mean (+/- se) of 32.8 cm (+/- 0.2) for fish that were later recaptured. Lengths of fish at recapture ranged between 22.9 cm and 76.2 cm with mean size of 41.9 cm (+/- 0.4). The minimum time at liberty for any fish between tagging and recapture was a single day while the maximum time at liberty was 10.3 years (3,748 days) (Figure 1). The mean time at liberty was 600 days (+/- 30). One fish was excluded from further analysis as its fork length at capture was not recorded. Seven fish were removed because the recapture date was not properly recorded. Of the remaining 431 fish recaptured, 394 were recaptured a single time, 35 fish were recaptured a total of two times, one fish recaptured 3 times, and two fish were recaptured 4 times. Further excluded from analysis were 46 individuals for whom time liberty was less than 60 days resulting in a data set of 387 unique individuals.

*Estimating Growth Parameters from Tagging Data*

*Parameter estimation using Bayesian inference*

The Bayesian hierarchical approach using the WinBUGS software yielded mean estimates of and L∞ for each of the Models 1-4 examined (Table 1). The presumptive optimal model which incorporated individual variability in both and (Model 1) yielded mean parameter estimates of = 0.32 and = 58.72 cm FL. The additional Models 2-4 suggest that individual variability in both and is important, with perhaps variability in being more important based upon the response of standard deviation from the base case of Model 1 to the constrained individual variability in Model 3 and Model 4 (Figure 2). Based upon parameter estimates and patterns of standard deviation, it is likely that Model 3 and Model 4 are not credible. Model 1 (preferred) and Model 2 perform similarly suggesting that the primary source of individual variability is due to variability in the L∞ growth parameter. Other Bayesian model specifications are presented in Appendix 2 for Model 1. The Gelman-Rubin convergence criteria indicated that the model solutions were credible, with asymptotic convergence clearly occurring after ~4000 iterations, well within the burn-in phase of the Bayesian modeling runs.

*Parameter estimation using maximum likelihood*

The maximum likelihood approach used for Model 5 successfully converged to produce estimates of (Table 3). Bootstrap confidence intervals (did/did not) encompass and parameters estimated using Bayseian methods. From these results, it was concluded that the maximum likelihood method produced satisfactory estimates relative to the Bayesian approach. Residuals values were distributed around zero fairly consistantly until recapture lengths exceeded 60 cm at which point the model predicted smaller recapture lengths than were observed (Figures 3 and 4). Models 6-12 fit using only training data successfully converged with parameter estimates reported in table 3. COMPARE MODEL 6 (TAG TRAIN) to MODEL 5 (TAG ALL)

*Comparing model performance*

The predictive variance metric for ensemble models fit using the training data ranged between 12.589 and 17.792 (mean = 13.904, se = 0.809). Two ensemble models (models 8 and 9) outperformed the model fit using only the tagging training data without the inclusion of additional data sources (model 6). These models had predictive variances of 12.592 and 12.589 respectively, compared to model 6’s variance of 12.792. Each of the models had similar residual patterns that were apparent in the model fit to the entire tagging data set, that is, they underestimated recapture length in the largest individuals. Bootstrapped parameter estimates fit across the full data set using the fitting methodology of models 8 and 9 are reported in table 1.

The predictive variance of growth models reported by other studies ranged between 12.725 and 281.759 (mean = 55.340, se = 17.545). Only one set of growth parameters, those estimated by Ralston and Miyamoto (1983) using analytical integration of otolith increments and fit without contstraining performed better than model 6 (Table 1). The same tendency to underestimate the length at recapture of the largest fish was present in the residual plots of the best fit models (Figures 3 and 4).

***Discussion***

Von Bertalanffy growth parameters are often used directly or indirectly in stock assessment and fisheries management (Haight, et al., 1993; Polovina, 1987). These efforts are sensitive to both growth parameters and the model used to estimate those parameters. For example, the rate of instantaneous natural mortality *M* is a value of interest often inferred using empirical relationships between *M* and (Ralston, 1987; Jensen, 1996; Thorson et al., 2017). Underestimating will underestimated *M*, characterizing a stock as being less productive than it actually is. If the management regime is linked to such a flawed estimate of stock productivity, then the stock is likely to be mismanaged and under harvested to its true biological potential. Conversely, an overestimation of leading to an overestimated M will tend to characterize a stock as more productive than it actually is and may lead to harvesting of stocks above sustainable levels. Therefore, accurate estimates of von Bertalanffy growth parameters are of much practical importance.

*Comparing Parameter Estimates*

The set of Von Bertalanffy parameter estimates, obtained without constraint to the parameter by Ralston and Miyamoto (1983) and those produced by Andrews et. al. (2012) most closely matched our results, with both and and values falling within the bootstrap confidence intervals estimated in this study (Table 1). Unsurprisingly, there was very close correlation between predicted length at recapture between the von Bertalanffy model fit with our parameters and the those fit in the respective studies.

Nearly all models failed to predict the length at recapture for the largest fish resulting in underestimations of size at recapture. This may be indicative that the species exhibits indeterminate growth and does not conform to a von Bertalanffy growth curve, particularly at larger sizes. Alternatively, it is possible that having reached a sufficient size, larger individuals are able to outcompete fish of smaller size classes for resources. Another explanation for the poor predictive ability at larger sizes may be sexual dimorphism. Age at length work conducted on the species from the Seychelles dimorphic growth with males reaching an asymptotic length of 85.8 cm compared to female asymptotic length of 77.6 cm and differing growth coefficients of 0.33 and 0.36 respectively (Hardman-Mountforrd et al. 1997, Mees 1993?). A method for externally sexing opakapaka has been recently described but was unknown at the time this mark recapture study was performed (Luers, Demartini 2017). As all models described in this study are sex agnostic, combining male and female cohorts may bias growth parameters, averaging growth parameters the sex composition of the data. If only one sex cohort attains the largest sizes, growth parameters pooled across both sexes will underestimate recapture lengths for the larger sex and overestimate recapture lengths in the smaller. Growth parameters from prior studies in the central pacific region appear to have been determined sex agnostic. Applied to both the training and full tagging data sets, parameters from these studies similarly under estimate the length of the largest fish. Future work to refine growth estimates for this species should consider the possibility that growth trajectories differ between males and females.

Compared to parameters reported by other studies of the species in the region, obtained estimates from tagging data were slightly lower for and slightly larger compared to all but one of the prior studies. Parameter confidence intervals overlapped the estimates of Ralston and Miyamoto’s unconstrained model fit (1983), estimates obtained by Andrews et al (2012) using radiochemistry and overlapped the confidence interval around estimates by DeMartini et al. (1994). Each of these studies relied on data from the previous studies to derive growth parameters, despite concern that integrated analytical aging methods may not have produced reliable age estimates. Interestingly, the work using ages obtained by this integrated analytical approach best predicted recapture lengths relative to all other parameter estimates previously published. The close compatibility with findings from this study suggest that these methodological concerns may be overstated.

Our confidence interval around overlapped the confidence interval obtained by O’Malley (2015) using the fitting method described by Francis. Interesting, the one study with more deviant parameter estimations was the only other to use mark recapture methods. While our confidence intervals around our respective growth estimates overlap, we report a larger value for the average maximum size attainable, and the Brody coefficient of growth *.*

The tagging study described here used opakapaka spanning 19.1 - 52.8 cm FL with a mean fish size of 37.0 cm FL. Hence this study focuses on fish that are 10 years of age and less (Figure 5). Assuming that opakapaka grow in a von Bertalanffy-like growth pattern, it is likely that the von Bertalanffy growth parameters presented here are well-estimated since the tagging data covers the region of maximum inflection of the growth trajectories. Recent work on opakapaka otoliths using lead-radium and bomb-radiocarbon dating has indicated that opakapaka live longer than previously thought, with ages exceeding 45 years for some individuals (Andrews et al., 2012). Such information is very important for grounding the upper end of the growth curve, which can be very uncertain since most growth curves utilize younger/smaller fish.

***Conclusion***

These results provide further support to studies that have used otoliths to validate individual age, through independent estimation of growth parameters, and a much larger sample size. As well, growth estimates from the Main Hawaiian Islands did not differ from recent estimates of growth from populations in the Northwestern Hawaiian Islands, though they do differ from those elsewhere in the species’ range. These findings are consistent with finding of broad genetic homogeneity across its distribution (Shaklee & Samollow, 1984; Gaither et al., 2010, 2011).As several methods employed here do not rely on age estimations for estimating growth parameters, they are not subject to concerns of bias from the episodic deposition of otolith material. Our results are highly consistent with and support results derived by radio-isotopic composition to validate individual age (Andrews et al. 2012). Our results also strongly agreed with growth estimates Ralston and Miyamoto fit without constraint to the term. In their work, they justified a constrained model based on the observation of the largest individual. In hindsight, similar to the argument presented by Francis (1988) and Sainsbury (1980), it seems problematic to constrain parameters describing a population mean based on measurements of the largest individual.

An underlying assumption when using mark-recapture methodologies to estimate growth is that initial capture and marking does not disrupt the growth of the individual. Estimates of individual growth between marking and recapture are highly consistent between the results of this study and those direct aging approaches. Had surgical implantation of marker tags disrupted individual growth, one would anticipate recapture sizes consistently less than those predicted with growth parameters from otolith-based studies, however the opposite appears to be the case. These results support for the utility of mark recapture methods applied to opakapakafor estimating growth rate parameters in other regions. However, the recapture rate in this study was approximately 10%. Low recapture rates may have been the result of large population sizes, trap shy behavior of individuals following marking, or high mortality of individuals following tagging due to predation, barotrauma, or other factors of disproportionate mortality. The effort to obtain each data point was roughly ten times that required by other methods, however analysis of data is substantially less involved than some other methods and describe observed rather than theoretical growth.

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(Gulland & Holt, 1959)