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

Scherrer, Stephen R.1\*

Kobayashi, Donald R.2

Weng, Kevin C.3

Okamoto, Henry Y.4

Oishi, Francis G.4

Franklin, Erik C.5

1University of Hawaii

Oceanography Department

1000 Pope Rd

Honolulu, Hawaii 96822

scherrer@hawaii.edu

2National Marine Fisheries Service

Pacific Islands Fisheries Science Center

1845 Wasp Blvd

Honolulu, Hawaii 96818

donald.kobayashi@noaa.gov

3Virginia Institute of Marine Science

College of William and Marry

*1375 Greate Road*

Gloucester Point, Virginia 23062

kevinweng@vims.edu

4Division of Aquatic Resources

State of Hawaii Department of Land and Natural Resources

1151 Punchbowl Street, Room 330

Honolulu, Hawaii 96813

5University of Hawaii

Hawaii Institute of Marine Biology

40-007 Lilipuna Rd

Kaneohe, Hawaii 96744

erik.franklin@hawaii.edu

\* Corresponding Author

***Abstract (175 Words)***

*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, von Bertalanffy growth function parameters were estimated from this tagging data. Direct aging and length frequency data from previous studies conducted on the species in the region were incorporated with tagging data to produce integrated estimates of growth using a maximum likelihood approach. Parameters estimated from tagging and integrated approaches provided better estimates of observed growth than those from prior 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 (500 Words)***

*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 often 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 fishery 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, parameter represents the theoretical age at which fork length is zero if the growth curve were extrapolated to the x-intercept and *t,* is a variable corresponding to the individual’s age at the time of sampling (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 includes individual length measurements and age estimates derived often from a morphological proxy (otoliths, scales, bones, spines). Accurate age estimations are important to avoid biasing growth estimates. In many tropical fishes, direct aging approaches may not perform well due to weak environmental seasonality, poorly-defined growth phase, or when growth of the proxy is not continuous. 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 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 length classes often overlap. Parameter estimates may be further confounded by protracted spawning, inter-annual variability in spawning and recruitment, and/or differential selectivity of sampling gear (Csirke, Caddy & Garcia, 1987).

Growth increment approaches where fish are captured, measured and tagged or otherwise 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 with growth characterized from the length of individuals at the time of marking () and recapture (), and the time at liberty ( between these two events.

Early work with applying Fabens method to tagging data failed to accommodate individual variability from mean growth of the population. Instead it was presumed that all individuals adhered to the same set of growth parameters and that the length of an individual at the time of tagging directly corresponded to its 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), temperature (Green & Fisher, 2004), oxygen levels (Pichavant Person-le-Ruyet, J., Le Bayon, N., Severe, A., Le Roux, A., Boeuf, G., 2001), genetics (Devlin et al., 2001), and other factors. Tagging, in and of itself, may affect a fish’s growth (Laurs and Wetherall, 1981). Failure to account for individual variability can introduce sever bias during estimation of growth parameters (Eveson, et al., 2007; Zhang, et al., 2009). Furthermore, growth estimates from tagging data were fundamentally incompatible with those from other approaches because early tagging approaches modeled 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 in tagging data and permit parameter comparisons across models fit with different approaches. A common solution is the introduction of an additional random variable, the age of an individual at tagging (Equation 3). By modifying the model in this way, growth observed in tagging data is a function of age rather than length, permitting comparison between tagging and direct aging methods (Eveson, Laslett & Polacheck, 2004). Inclusion of this term also reduces bias and accommodates modest measurement errors during parameter estimation (James, 1991; Palmer, Phillips & Smith, 1991; Wang, Thomas & Somers, 1995; Laslett, Eveson & Polacheck, 2002; Zhang, Lessard & Campbell, 2009).

Alternative procedures for model fitting 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). Approaches using maximum likelihood and Bayesian fitting procedures model growth at a population levels from distributions representing individual level parameters (Francis, 1988b; Kimura, Shimada & Lowe, 1993; Wang, Thomas & Somers, 1995; Zhang, Lessard & Campbell, 2009). The flexibility of Bayesian approaches allows both and to be sampled in this manner and can account for prior information while estimating parameters (Zhang, Lessard & Campbell, 2009). Maximum likelihood approaches typically treat as a fixed effect and as random, though omission of this second source of variability does not bias parameters??? (Wang, Thomas & Somers, 1995; Laslett, Eveson & Polacheck, 2002)More complex maximum likelihood models allow for reconciliation of direct aging, length frequency, and growth increment approaches to estimate a single set of growth parameters integrating more than one data type (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 (Sundberg & Underkoffler, 2009; “Hawaii Reported Landing Tables,” 2016). Due to its economic and cultural significance, a great amount of effort has been expended by number of studies 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). In Hawaii, prior growth estimates for opakapaka have been obtained primarily from length at age data using otolith growth increments (Ralston & Miyamoto, 1983; Uchiyama & Tagami, 1984; Radtke, 1987; Demartini, Landgraf & Ralston, 1994, Ralston & Williams, 1988). However, age estimates obtained using bomb radiocarbon dating of otoliths obtained from 33 individuals from the North Western Hawaiian Islands indicated that individual longevity can 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). Furthermore, recent work has shown that poor definition of the earliest otolith growth annuli can lead to significantly different estimates of opakapaka age between readers (Wakefield et al. 2017). Growth parameters have also been estimated using length frequency of juvenile cohorts sampled in a known nursery, however this analysis did not consider effects of individual variability by using 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). 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 using growth increment approaches. Growth parameter estimates differed significantly from one another and from prior growth studies (O’Malley, 2015). These discrepancies may stem from the limited size range of recaptured individuals and the use of model forms incompatible with those used by other studies.

*Objective*

In this analysis, von Bertalanffy growth parameters are estimated from *P. filamentosus* tagging data collected in the Main Hawaiian Islands usingBayesian and maximum likelihood fitting procedures. A series of models integrating length at age and length frequency data previously used to describe growth for the species are then developed and tested to determine a preferred model structure. Composite growth parameters are then estimated for *P. filamentosus* using the preferred model structure and the predictive capability of these growth parameters are compared to those reported previously. This study differs from previous work as it quantifies growth parameters from a previously unreported tagging data set and reconciles additional sources of data representing 30+ years of work to produce a single set of growth parameters for *P. filamentosus* in the Hawaii region.

***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 opakapaka around the Main Hawaiian Islands.

Fish were caught with hook-and-line 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 to ascertain survival likelihood. 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 appearing lively and upright were deemed likely to survive and thus suitable candidates for tagging. These fish were surgically implanted with unique identifiable internal anchor tags with a monofilament streamer protruding from the incision in the peritoneal cavity. The fork length of each fish measured to the nearest ¼ inch was recorded before the fish was returned headfirst to sea 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 OTP personnel were outfitted with an additional tag following procedures similar to during initial capture. For each individual, the location of capture (DAR statistical reporting grid), length at tagging, and date of capture was recorded. 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 were removed from the dataset if they were not the of species of interest, if no recapture was reported, or for if there was no record of the tag identification number. Fork lengths for the remaining fish recorded at tagging and recapture were linearly transformed from inches to centimeters prior to model fitting. Observed growth () and time at liberty (), were calculated for each fish. 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 violate assumptions of independence. Fish with less than 60 days were excluded from the dataset.

*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 the *ith* individual. 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 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 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 and , but with the added feature of estimating ages at initial tagging within the Bayesian framework (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 fit using non-linear least squares 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 of the Bayesian approach in that asymptotic length, , describes the distribution of the asymptotic lengths of each individual , and is treated as a random effect while is treated as a fixed unknown parameter. The distribution of is treated as normal with a mean and standard deviation , accounting for individual deviation from the population mean. Rather than using length increments to fit observed growth, a bivariate normal joint distribution describing the lengths recorded at marking and recapture are used to estimate each individual’s age at tagging (See Laslett et. al., 2002 for the full method for deriving individual joint distributions). describes the distribution of individual s and is treated random effect with a distribution . The distribution of is assumed to be lognormal with mean and standard deviation . Measurement error is also treated as a random normal distribution N. An unconditional joint density is then derived for each individual by integrating the joint distribution with respect to (E6).

Growth function parameters are estimated through minimizing of the negative log-likelihood function obtained by summing the unconditional joint density of each individual (E7).

This approach was used to estimate the parameters , , , , , and . Two-sided confidence intervals (2.5%, Median, 97.5%) were estimated from the distribution of each parameter following 10,000 successful bootstrap iterations. For each iteration, the model was refit on a bootstrapped data set of equal length to and comprised of the original tagging data sampled at random with replacement.

*Estimation of Ensemble Growth Parameters*

Datasets previously used to estimate growth for opakapakasampled from the Main and Northwestern Hawaiian Islands, across a range of size classes, were used to produce a single set of parameter estimates using a modified form of the integrated method proposed by Eveson, Laslett, Polachek (2004). Additional datasets represented both direct aging and length frequency approaches. Sources of direct ageing data consisted of four previously reported length at age datasets from three studies. Individual ages for these data were estimated by analytical integration of the width of otolith annuli (Ralston and Miyamoto, 1983, n = 65), counts of otolith micro increments (Demartini et al., 2014, n = 35), 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), and the lead-radium ratios of individuals pooled by size class (Andrews et al., 2012, n = 3).

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 corresponded to the height of one additional fish. Using this method to extrapolate monthly length frequency data resulted in a total count of 1,048 individuals while in the original study reports 1,047 (Moffitt & Parrish, 1996).

The reconstructed length frequency data was incorporated into ensemble models using the two-step method described in Laslett et al 2004. During the first step, a Gaussian mixture model was 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 the observed mode. A bimodal Gaussian mixture model was fit for the months of October-Feb, as the original study reports two cohorts were reported present during these periods, while a single cohort was present 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 . For simplicity, cohort age is the difference in years between the 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. July is the month of peak spawning for opakapaka (Luers, Demartini & B, 2017) which resulted in age estimates between 3 and 19 months. 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. This method is discussed to greater depth 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 are 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 annuli widths (Ralston & Miyamoto, 1983). The second dataset consisted of juvenile fish aged using the total count of daily 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 of three size classes (Andrews et al., 2012).

The method for estimating growth parameters from direct aging data components icn be found 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 when a fish has a hypothetical length of zero. As with the model for tagging data, is the individual asymptotic length of thefish drawn from the random normal distribution . represents the distribution of individual measurement error and is similarly random, drawn from the population distribution . Equation 15 describes the log-likelihood function derived from these equations.

An appropriate overall objective likelihood function (E16) is then defined from the sum of the negative log-likelihood functions for direct aging, length frequency, and growth increment approaches, each with its own scaling constant, . A single set of growth parameters best describing the data can then be obtained by minimizing the objective likelihood function.

By manipulating the value of scaling constants, how similar datasets were treated, and which datasets were included, six model structures were developed and evaluated (Table 2). Two approaches were used to define the scaling constants. The first equally weighted each likelihood function so that each data source had 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 ().

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 considered independently and assigned their own log-likelihood function or if these data sources were pooled and contributed to estimation of a single log-likelihood function. Omission of direct aging data where ages were estimated using counts of otolith annuli was also considered as this method is known to be unreliable for opakapaka (Wakefield et al 2017) (Table 2).

*Comparing model performance*

The structure of models 6-12 were evaluated using the following a repeated learning-testing cross validation procedure (Burman, 1989) to determine which combination of model weighting, data pooling, and data sources parameter estimates that best predicted observed growth from tagging data. Each model structure was trained using thirds of the tagging data (n = 258) selected at random while the remaining third (n = 129) was reserved for evaluating each model’s predictive ability. Model performance was evaluated using and parameter estimates, length at tagging, and time at liberty of each individual in the validation set to predict their length at recapture using Equation 2. The variance (between the predicted ( and observed (length of each fish recapture (E17) was used as a metric for comparing the performance of competing model structures.

The preferred model structure was the one whose estimated parameters most frequently produced the smallest variance. This procedure was repeated 1,000 times. During each iteration, parameter estimates reported previously (table 1) were also scored using the variance metric and compared one another and to ensemble models.

Following this, the model structure that best predicted observed growth most frequently was refit using the entire data set. Two-sided 95% confidence intervals were estimated for each parameter from the results of 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. 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 (mean = 32.8 cm +/- 0.24) and ranged from 19.1 cm and 52.8 cm (mean = 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 (mean = 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 yielding 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 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 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 of parameters and overlapped and parameters from Bayseian models 1 and 2. From these results, it was concluded that estimates produced by maximum likelihood were satisfactorily similar to estimates from the Bayesian approach. Model residuals were distributed around zero fairly consistantly for all but the largest fish. For fish with recapture lengths exceeing 60 cm, growth models underestimated observed recapture lengths (Figures 3 and 4).

*Comparing model performance*

Across all 1,000 iterations to determine model structure, the cross validation variance metric ranged between 12.589 and 17.792 (mean = 13.904 +/- 0.809). Only three models were ever the prefered model structure that best predicted the observed growth in validation data. The prefered model sturcture which outperformed alternative model structures in 57% of the cross validation iterations was Model 11 (mean = +/-). Bootstrapped parameter estimates fit using this model structure and all available tagging data set are summarized in table 1 and reported in full in table 3. The second best model structure was that of model 7 and was the best fit model in 42% of cross validation iterations (mean = +/-) while Model 9 was the prefered model structure in only 1% of cross validation iterations (mean = +/- ). When fit to the entire tagging data set, each model structure had a similar residual pattern to model 5 where recapture length of the largest individuals was underestimated.

The predictive variance of growth models reported by other studies ranged between 12.725 and 281.759 (mean = 55.340 +/- 17.545). Model 6, the model structure which considered only tagging data, never outperformed model structures that included direct aging and length frequency data, however it did outperform previously reported parameters in XXX of XXXX iterations. Only one set of growth parameters, those estimated by Ralston and Miyamoto (1983) using analytical integration of otolith annuli and fit without contstraining performed better than model 6 (Table 1). Growth parameters estimated by Ralston and Miyamoto (1983) without constraint to outperformed other literature parameter estimates in XXX of XXXX iterations. The next best models were TK with XXX of XXX and TK with XXX of XXX. Previously estimated growth parameters exhibited the similar tendency to underestimate the length at recapture of the largest fish as models fit in this study (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 underestimate *M*, characterizing a stock as 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 can lead to overharvesting of a stock when it is believed to be more productive than it actually is. 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, however it is interesting to note that length at data from Ralston and Miyamoto where age was estimated using otolith annuli were not included in the preferred model structure.

Nearly all models, here and from previous studies, underestimated the length at recapture for the largest fish. This may be an indication that the species exhibits indeterminate growth and does not readily conform to a von Bertalanffy growth curve. It may be that, having reached a sufficient size, larger individuals are able to outcompete fish of smaller size classes for resources. Another possible explanation for the poor predictive ability at larger sizes is sexual dimorphism. Age-at-length and length frequency data conducted on the species in the Seychelles describe dimorphic differences in growth between sexes with a mean asymptotic length of 85.8 cm for males versus 77.6 cm for females and respective growth coefficients of 0.33 and 0.36 (Mees, 1993; Hardman-Mountford, Polunin & Boulle, 1997). A method for externally sexing opakapaka has been recently described but was unknown at the time this mark recapture study was performed (Luers, Demartini & B, 2017) and thus all models fit in this study are sex agnostic, combining male and female data. If the sex ratio of fish attaining the largest sizes classes is not representative of the sex ratio across all size classes, growth parameters estimated in this way will underestimate recapture lengths for the sex attaining the largest sizes and overestimate recapture lengths in the other. Prior estimations of growth parameters for opakapaka in the Central Pacific region appear to have been determined without consideration to sex and similarly underestimate growth in the largest of fish. Future work to refine growth estimates for opakapaka should consider the possibility that growth trajectories may differ between males and females of this species.

Parameters obtained solely from tagging data using Bayesian and maximum likelihood approaches resulted in lower estimates of and larger estimates of compared to those of ensemble models and all but one prior study (WHICH?). It is likely underrepresentation of the largest size classes in the tagging data resulted in growth curves with a premature asymptote. Parameter estimates from ensemble models inclusive of the largest fish from length at age data better predicted growth than those fit with only tagging data in every case and, on this basis, likely provide better estimates for the species.

Parameter confidence intervals for parameters of the preferred ensemble model fit 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 studies previous to derive growth parameters, despite concern that integrated analytical aging methods may not have produced reliable age estimates. Despite concerns regarding the accuracy of age estimates from otolith annuli, relative to previous studies in the region, the study using this method was best predicted the growth observed, however, the preferred model structure omitted this data from the parameter estimation procedure.

Model 5’s confidence interval around overlapped the confidence interval obtained by O’Malley (2015) using the fitting method described by Francis. While our confidence intervals around our respective growth estimates overlap, we report a larger value for the mean asymptotic size, and the Brody coefficient of growth*.* These discrepancies may result from the greater size range of individuals in this study or use of a model structure where data were used to fit growth parameters using age rather than length.

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. The tagging data described here includes opakapaka with fork lengths at capture spanning 19.1 - 52.8 cm and a mean size of 37.0 cm. This data corresponds to fish mean ages between 1.5 and 7 years (Figure 5). Assuming opakapaka grow in a von Bertalanffy-like pattern, it is likely that ensemble growth parameters presented here are well-estimated as they incorporate data from the largest size classes from the direct-aging components as well as from the smallest juvenile fish in the length frequency component.

***Conclusion***

These results reconcile previously unreported growth-increment data with direct-age and length frequency data from previous studies to estimate holistic growth parameters spanning much of the life history of the species. Growth estimates from data collected in the Main Hawaiian Islands did not differ from those reported from populations in the Northwestern Hawaiian Islands, though they do differ from those elsewhere in the species’ range. These findings are consistent broad genetic homogeneity across the species’ distribution in the Central Pacific (Shaklee & Samollow, 1984; Gaither et al., 2010, 2011).Holistic parameter estimates derived from ensemble models that incorporating length frequency and length at age data are better able to predict growth and are highly consistent with and support results derived by radio-isotopic composition to validate individual age by Andrews et al. (2012) as well as the approach of Ralston and Miyamoto (1983) fit without constraint to the .

An underlying assumption when using mark-recapture methodologies to estimate growth is that the act of tagging 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. This was not the case. Estimated von Bertalanffy parameters underestimated growth in the largest fish. We speculate this may be the result of dimorphic growth between sexes and should be accounted for in future attempts to refine growth parameters for the species. 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 tagging, or high mortality of tagged individuals 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 approaches, however analysis of data is substantially less involved than some other methods and describe observed growth, useful for validating growth estimates.

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**References**

Allen GR. 1985. Fao Species Catalogue Vol . 6 . Snappers of the World. *Fao Fisheries Synopsis* 6:208. DOI: 10.1016/0025-326X(92)90600-B.

Andrews a H., DeMartini EE., Brodziak J., Nichols RS., Humphreys RL. 2012. A long-lived life history for a tropical, deepwater snapper (Pristipomoides filamentosus): bomb radiocarbon and lead-radium dating as extensions of daily increment analyses in otoliths. *Canadian Journal of Fisheries and Aquatic Sciences* 69:1850–1869. DOI: 10.1139/f2012-109.

Andrews AH., Humphreys R l., DeMartini ED., Nichols RS., Brodziak J. 2011. Bomb Radiocarbon and Lead-Radium Dating of Opakapaka (Pristipomoides filamentosus). *Fisheries Science*.

Benaglia T., Chauveau D., Hunter DR., Young D. 2009. Mixtools: An R package for analyzing finite mixture models. *Journal of Statistical Software* 32:1–29.

Bennett JT., Boehlert GW., Turekian KK. 1982. Confirmation of longevity in Sebastes diploproa (Pisces: Scorpaenidae) from 210Pb/226Ra measurements in otoliths. *Marine Biology* 71:209–215. DOI: 10.1007/BF00394632.

Burman P. 1989. A comparative study of ordinary cross-validation, v-fold cross-validation and the repeated learning-testing methods. *Biometrika* 76:503–514. DOI: 10.1093/biomet/76.3.503.

Campana SE. 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *Journal of Fish Biology* 59:197–242. DOI: 10.1006/jfbi.2001.1668.

Chen Y., Jackson DA., Harvey HH. 1992. A Comparison of von Bertalanffy and Polynomial Functions in Modelling Fish Growth Data. *Canadian Journal of Fisheries and Aquatic Sciences* 49:1228–1235. DOI: 10.1139/f92-138.

Csirke J., Caddy JF., Garcia S. 1987. Methods of size-frequency analysis and their incorperation in programs for fish stock assessment in developing countries. In: Pauly D, Morgan GR eds. *Length-Based Methods in Fisheries Research*. Manila, Philippines and Safat, Kuait: The International Center for Living Aquatic Resources Management, 1–6.

Demartini EE., Landgraf KC., Ralston S. 1994. A Recharacterizatinon of the age-length and growth relationships of Hawaiian snapper Pristipomoides filamentosus. :1–19.

Devlin RH., Biagi CA., Yesaki TY., Smailus DE., Byatt JC. 2001. Growth of domesticated transgenic fish: A growth-hormone transgene boosts the size of wild-but not domesticated trout. *Nature* 409:781–782. DOI: 10.1038/35057314.

Eveson JP., Laslett GM., Polacheck T. 2004. An integrated model for growth incorporating tag–recapture, length–frequency, and direct aging data. *Canadian Journal of Fisheries and Aquatic Sciences* 61:292–306. DOI: 10.1139/f03-163.

Eveson JP., Polacheck T., Laslett GM. 2007. Consequences of assuming an incorrect error structure in von Bertalanffy growth models: a simulation study. *Canadian Journal of Fisheries and Aquatic Sciences* 64:602–617. DOI: 10.1139/f07-036.

Fabens AJ. 1965. Properties and fitting of the von Bertalanffy growth curve. *Growth* 29:265–289.

Francis RICC. 1988a. Are Growth Parameters Estimated from Tagging and Age–Length Data Comparable? *Canadian Journal of Fisheries and Aquatic Sciences* 45:936–942. DOI: 10.1139/f88-115.

Francis RICC. 1988b. Maximum likelihood estimation of growth and growth variability from tagging data. *New Zealand Journal of Marine and Freshwater Research* 22:43–51. DOI: 10.1080/00288330.1988.9516276.

Gaither MR., Jones S a., Kelley C., Newman SJ., Sorenson L., Bowen BW. 2011. High connectivity in the deepwater snapper Pristipomoides filamentosus (lutjanidae) across the indo-pacific with isolation of the Hawaiian archipelago. *PLoS ONE* 6. DOI: 10.1371/journal.pone.0028913.

Gaither MR., Toonen RJ., Sorenson L., Bowen BW. 2010. Isolation and characterization of microsatellite markers for the crimson jobfish, pristipomoides filamentosus (Lutjanidae). *Conservation Genetics Resources* 2:169–172. DOI: 10.1007/s12686-009-9119-3.

Gelman A., Rubin DB. 1992. lnference from Iterative Simulation Using Multiple Sequences. *Statistical Science* 7:457–472. DOI: 10.2307/2246093.

Green BS., Fisher R. 2004. Temperature influences swimming speed, growth and larval duration in coral reef fish larvae. *Journal of Experimental Marine Biology and Ecology* 299:115–132. DOI: 10.1016/j.jembe.2003.09.001.

Gulland JA., Holt SJ. 1959. Estimation of growth parameters for data at unequal time intervals. *ICES Journal of Marine Science* 25:47–49. DOI: 10.1093/icesjms/25.1.47.

Hardman-Mountford NJ., Polunin NVC., Boulle D. 1997. Can the age of the tropical species be determined by otolith measurement?: a study using Pristipomoides filamentosus (Pisces: Lutjanidae) from the Mahe Plateau, Seychelles. *Naga, The ICLARM Quarterly* 20:27–31.

Hawaii Reported Landing Tables 2016. *Available at* *https://www.pifsc.noaa.gov/wpacfin/hi/dar/Pages/hi\_data\_3.php* (accessed March 23, 2018).

James IR. 1991. Estimation of von Bertalanffy growth curve parameters from recapture data. *Biometrics* 47:1519–1530. DOI: 10.2307/2532403.

Jensen AL. 1996. Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival. *Canadian Journal of Fisheries and Aquatic Sciences* 53:820–822. DOI: 10.1139/f95-233.

Kerrigan BA. 1994. Post-settlement growth and body composition in relation to food availability in a juvenile tropical reef fish. *Marine Ecology Progress Series* 111:7–15. DOI: 10.3354/meps111007.

Kimura DK., Shimada AM., Lowe SA. 1993. Estimating von Bertalanffy growth parameters of sablefish Anoplopoma fimbria and Pacific cod Gadus macrocephalus using tag-recapture data. *Fishery Bulletin* 91:271–280.

Kobayashi DR., Okamoto HY., Oishi FG. 2008. Movement of the deepwater snapper opakapaka , Pristipomoides filamentosus , in Hawaii : Insights from a large-scale tagging program and computer simulation.

Laslett GM., Eveson JP., Polacheck T. 2002. A flexible maximum likelihood approach for fitting growth curves to tag-recapture data. *Canadian Journal of Fisheries and Aquatic Sciences* 59:976–986. DOI: 10.1139/f02-069.

Luers MA., Demartini EED., B RLHJ. 2017. Seasonality , sex ratio , spawning frequency and sexual maturity of the opakapaka Pristipomoides filamentosus ( Perciformes : Lutjanidae ) from the Main Hawaiian Islands : fundamental input to size-at-retention regulations. *Marine and Freshwater Research*. DOI: 10.1071/MF17195.

Maller RA., Deboer ES. 1988. An analysis of two methods of fitting the von bertalanffy curve to capture-recapture data. *Marine and Freshwater Research* 39:459–466. DOI: 10.1071/MF9880459.

Mees CC. 1993. Population biology and stock assessment of Pristipomoides filamentosus on the Mahe Plateau, Seychelles. *Journal of Fish Biology* 43:695–708. DOI: 10.1111/j.1095-8649.1993.tb01147.x.

Moffitt RB., Parrish FA. 1996. Habitat and life history of juvenile Hawaiian pink snapper, Pristipomoides filamentosus. *Pacific Science* 50:371–381.

O’Malley J. 2015. A Review of the Cooperative Hawaiian Bottomfish Tagging Program of the Pacific Islands Fisheries Science Center and the Pacific Islands Fisheries Group. :47. DOI: 10.7289/V59W0CF7.

Okamoto HY. 1993. *Develop Opakapaka tagging techniques to assess movement behavior*.

Palmer MJ., Phillips BF., Smith GT. 1991. Application of nonlinear models with random coefficients to growth data. *Biometrics* 47:623–635. DOI: 10.2307/2532151.

Patterson WF., Cowan JH., Wilson C a., Shipp RL. 2001. Age and growth of red snapper, *Lutjanus campechanus*, from an artificial reef area off Alabama in the northern Gulf of Mexico. *Fishery Bulletin* 99:617–627.

Pichavant Person-le-Ruyet, J., Le Bayon, N., Severe, A., Le Roux, A., Boeuf, G. K. 2001. Comparative effects of long-term hypoxia on growth, feeding and oxygen consumption in juvenile turbot and Eruopean sea bass. *Journal of Fish Biology* 59:875–883.

R Core Team. 2014. R: A Language and Environment for Statistical Computing.

Radtke RL. 1987. Age and growth information available from the otoliths of the Hawaiian snapper, Pristipomoides filamentosus. *Coral Reefs* 6:19–25. DOI: 10.1007/BF00302208.

Ralston SVD. 1987. Mortality rates of snappers and groupers. *Tropical snappers and groupers: biology and fisheries management*:375–404.

Ralston S., Miyamoto GT. 1983. Analyzing the width of daily otolith increments to age the Hawaiian snapper, Pristipomoides filamentosus. *Fishery Bulletin* 81:523–535.

Sainsbury KJ. 1980. Effect of individual variability on the von Bertalanffy growth equation. *Canadian Journal of Fisheries and Aquatic Sciences* 37:241–247. DOI: 10.1139/f80-031.

Shaklee JB., Samollow PB. 1984. Genetic variation and population structure in a deepwater snapper, Pristipomoides filamentosus, in the Hawaiian Archipelago. *Fishery Bulletin* 82:703–713.

Spiegelhalter D., Thomas A., Best N., Way R. 2003. WinBUGS User Manual. *Components* 2:1–60. DOI: http://www.mrc-bsu.cam.ac.uk/wp-content/uploads/manual14.pdf.

Sundberg M., Underkoffler K. 2009. Size Composition and Length ‐ Weight Data for Bottomfish and Pelagic Species Sampled at the United Fishing Agency Fish Auction in Honolulu , Hawaii from October 2007 to December 2009.

Thorson JT., Munch SB., Cope JM., Gao J. 2017. Predicting life history parameters for all fishes worldwide. *Ecological Applications* 27:2262–2276. DOI: 10.1002/eap.1606.

Uchiyama JH., Tagami DT. 1984. Life history, distribution, and abundance of bottomfishes in the Northwestern Hawaiian Islands. In: Grigg RW, Tanoue KY eds. *Proceedings of the Second Symposium on Resource Investigations in the Northwestern Hawaiian Islands*. 229–247.

Wang Y-G., Thomas MR., Somers IF. 1995. A maximum likelihood approach for estimating growth from tag–recapture data. *Canadian Journal of Fisheries and Aquatic Sciences* 52:252–259. DOI: 10.1139/f95-025.

Zhang Z., Lessard J., Campbell A. 2009. Use of Bayesian hierarchical models to estimate northern abalone, Haliotis kamtschatkana, growth parameters from tag-recapture data. *Fisheries Research* 95:289–295. DOI: 10.1016/j.fishres.2008.09.035.

(Gulland & Holt, 1959)