***Revised growth estimates for Pristipomoides filamentosus in the Hawaiian Islands using mark-recapture studies, Bayesian analysis, and integrative data approaches***

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***Abstract (175 Words Max)***

*Pristipomoides filamentosus* is an economically and culturally important species of deep-water snapper in the Hawaiian archipelago. From 1989 to 1993, the State of Hawaii conducted a fisher participation mark-recapture study to quantify growth and other life history parameters for the species. Over a span of approximately 10 years, 10.3% of 4,179 tagged fish were recaptured. We compared von Bertalanffy growth parameter estimates obtained using Bayesian and maximum likelihood approaches to those previously reported for the species. Direct aging and length frequency data used in other published regional growth studies were incorporated to produce integrated estimates of growth. Results from our preferred integratived model reconcile 30+ years of effort from various methods to estimate growth parameters ( = 67.55 cm FL and K = 0.219) and demonstrate the importance of individual variability in *P. filamentosus* due primarily to the asymptotic length parameter . These results also point to the importance of incorporating very large fish when estimating parameters and the possibility of sexually dimorphic growth in the species. These results have management implications as growth is often an input for age-based stock assessment models and used as a proxy for other life history traits.

***Introduction (500 Words)***

*Pristipomoides filamentosus* (Valenciennes, 1830) is a species of long-lived deep-water snapper distributed throughout the tropical Pacific and Indian Oceans (Allen 1985, Andrews et al. 2012). Known as opakapaka in Hawaii, the species constitutes a significant fraction of the Hawaiian commercial bottomfish fishery, which targets a complex of 6 snapper and 1 species of one grouper (Ralston and Polovina 1982, “Hawaii Reported Landing Tables” 2016)(Langseth 2018). While the current stock assessment for this fishery used a surplus production model for the entire complex, there is interest in the potential use of species-specific, age-structured assessments that require improved life history studies of age and growth in bottomfish (Langseth et al. 2018).)

Growth parameters have been estimated for *P. filamentosus* using a variety of methods in Hawaii and elsewhere (Table 1). Parameter estimates were determined using direct aging approaches 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 relying on counts of otolith annuli may be biased due to episodic growth and/or poor increment resolution in early (< 5 years) life stages (Andrews et al. 2012, Wakefield et al. 2017). Growth was also estimated using modal progression during a length frequency study targeting juvenile fish (< 2 years) but did not consider individual variability when extrapolating growth to larger size classes (Moffitt and Parrish 1996). Preliminary results of an ongoing tagging study have been limited by the size distribution of recaptured individuals and use model parameterizations incompatible with other methods for determining growth (O’Malley 2015). While these studies produced individual estimates of growth parameters, none of them holistically integrated data from the various methods to explicitly evaluate the parameter values and sources of uncertainty.

Analytical and statistical advances to methods for estimating growth have been developed to account for sources of variability and permit parameter comparisons across length-at-age, length frequency, and tagging based approaches. Structural modifications to Fabens (1965) parameterization of the von Bertalanffy growth model address issues of compatibility between growth parameters estimated from tagging studies and other methods, and can reduce bias through the accommodation of modest measurement errors (Francis 1988, Maller and Deboer 1988, James 1991, Palmer et al. 1991, Wang et al. 1995, Laslett et al. 2002, Eveson et al. 2004, 2007, Zhang et al. 2009). Maximum likelihood and Bayesian model fitting procedures accommodate individual growth variability by describing population parameters using probability distributions (Francis 1988, Kimura et al. 1993, Wang et al. 1995, Zhang et al. 2009). The flexibility of Bayesian approaches allow and to be sampled in this manner and can account for prior information when estimating parameters. Maximum likelihood approaches typically treat as a fixed effect but flexibility in their implementation has allowed for the development of model structures that can estimate a single set of growth parameters from direct aging, length frequency, and growth increment data simultaneously (Wang et al. 1995, Laslett et al. 2002, Eveson et al. 2004, Zhang et al. 2009).

Here previously unreported tagging data are used to estimate growth parameters for *P. filamentosus* usingBayesian and maximum likelihood procedures. A series of models integrating previous length-at-age and length frequency data with the tagging data are developed to describe growth across most of the species’ life history. Models are tested to determine a preferred model structure. New growth parameters are estimated and compared to those previously reported for the Hawaiian Archipelago.

***Methods***

*Study Domain/Setting?*

*Opakapaka Tagging Program*

Tagging data used for this analysis were obtained by Hawaii’s Division of Aquatic Resources (DAR) within the state’s Department of Land and Natural Resources (DLNR). Between 1989 and 1994 the Opakapaka Tagging Program (OTP), led by staff biologist Henry Okamoto and operating from fishing vessels contracted out of Honolulu Harbor, targeted and tagged *P. filamentosus*. Over the study’s duration, OTPtagged 4,179 juvenile and adult *P. filamentosus* around the Main Hawaiian Islands.

Fish were caught with hook-and-line gear and brought 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.

There were 487 recaptures recorded forfor 432 unique individuals for a recapture rate of 10.3% of tagged fish. Recaptures of marked *P. filamentosus* were reported up to a decade after tagging with the most recent fish reported in October of 2003 (Okamoto 1993, Kobayashi et al. 2008). Individuals recaptured by OTP personnel were outfitted with an additional tag following procedures similar to their initial capture. For each individual, the location of capture (DAR statistical reporting grid), length at tagging, and date of capture were 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, depth, fork length, and date that tagged fish were landed with a $10 reward.

*Tagging Data Management*

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 correct species of interest, if no recapture was reported, or if there was no record of the tag identification number. Fork lengths for the remaining fish recorded at tagging and recapture were 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. This was done because growth recorded during this window of time was thought to be more likely the result of measurement error. Applying this filter removed nearly all fish for which negative growth was reported.

*Parameter Estimation from Tagging Data: Bayesian Approach*

Growth parameters were estimated for the *P. filamentosus* tagging data following the Bayesian methodology of Zhang et al. (2009). 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 provided 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 used a fixed parameter while allowing the parameter to vary across individuals. Model 3 used a fixed parameter while allowing the parameter to vary across individuals. Lastly, Model 4 used 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. 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. Inclusion of the term represents a significant improvement over prior methods by modeling growth as a function of age, rather than observed length, allowing growth parameters to be compared between models using tagging data and length-at-age methods (Wang et al. 1995). Model 1 is the presumptive best estimate for *P. filamentosus* 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 (Table 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 Table 2. Convergence was also ascertained by examination of the Gelman-Rubin statistic (Gelman and 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.

*Parameter Estimation from Tagging Data: Maximum Likelihood Approach*

Model 5 was fit using the maximum likelihood approach of Laslett, Everson, & Polacheck (2002) using Equation 2.

This method derived growth parameters from the joint distribution of an individual’s length at tagging and recapture to estimate growth parameters. This approach was most similar to model 2 of the Bayesian approach in that asymptotic length, , was treated as a normal random effect while was treated as a fixed unknown parameter. The distribution of was 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 of lengths recorded at marking and recapture was used to estimate each individual’s age at tagging . The distribution of individual s is and is treated as a random effect with a lognormal distribution . Measurement error was also treated as a random normal distribution . An unconditional joint density was then derived for each individual by integrating their individual joint distribution with respect to . A detailed description of this process is described by Laslett et. al. (2002).

Growth function parameters were estimated through minimizing of the negative log-likelihood function obtained by summing the unconditional joint density of each individual (E3).

This approach was used to estimate values of the parameters , , , , and . Two-sided 95% confidence intervals (2.5%, Median, 97.5%) were then estimated from the distribution of each parameter following 10,000 successful bootstrap iterations to obtain population parameters. For each bootstrap iteration, the model was refit on data randomly resampled from the original tagging data with replacement.

*Estimation of Integrative Growth Parameters using sources of growth data*

Datasets previously used to estimate regional growth for *P. filamentosus* in the Main and Northwestern Hawaiian Islands and our tagging data from the Main Hawaiian Islands were used to produce a single set of parameter estimates using a modified form of the integrated method proposed by Eveson, Laslett, and Polachek (2004). This approach leverages additional data to estimate growth parameters that may provide more robust estimates of and . Additional datasets that were included represent both direct aging and length frequency approaches.

*Parameter Estimation: Length Frequency Data*

Length frequency data consisted of the size distributions of juvenile *P. filamentosus* sampled over 13 months between October 1989 and February 1991 reported by Moffitt and Parrish (1996). The reported fork length of captured fish was binned by 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 month of sampling was determined by overlaying a series of evenly spaced horizontal lines across the Y-axis of each histogram corresponding to the addition of a single fish. Using this method to reconstruct monthly length frequency data resulted in a total count of 1,048, individuals while the original study reported 1,047 (Moffitt and Parrish 1996).

The reconstructed length frequency data were incorporated into integrative models using the two-step method described in Laslett et al 2002. 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-February, as the original study reported that two cohorts were present during this period, 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 used to estimate growth parameters (E4).

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 . July is the month of peak spawning for *P. filamentosus* (Luers et al. 2017) which resulted in age estimates between 3 and 19 months. Sampling and residual model errors were described using random normal distributions and respectively. In contrast to tagging and direct aging components, there is a dearth of information available to estimate the variance component of asymptotic length, using length frequency methods, so this term was modeled as fixed effect, . From this, the expected mode fork length of each cohort (E6), and associated variability during each sampling period (E7) were calculated and used to construct the negative log likelihood function (E8). The rationale for these approximations is discussed to greater depth in Eveson et al. 2004.

*Parameter Estimation: Direct Aging Data*

Sources of direct ageing data consisted of four previously reported length-at-age datasets from three studies. Age estimates for length at age data were obtained through analytical integration of otolith annuli width (Ralston and Miyamoto, 1983, n = 65), counts of otolith micro increments (Demartini et al., 2014, n = 35), comparison of bomb radiocarbon derived C14:C12 ratios in otoliths to a standard reference obtained from hermatypic coral cores from the Hawaiian Archipelago (Andrews et al., 2012, n = 33), and the lead-radium ratios of individuals pooled by size class (Andrews et al., 2012, n = 3).

The details of the method for estimating growth parameters from direct aging data components are described in Eveson et al. 2004. Briefly, parameters were modeled using the VBGF model described by equation E9.

Expected length for each individual and the variance of the measurement error was described by equations E10 and E11.

Where denoted the length of the fish*,* at age and was a fixed parameter analogous to when a fish has a hypothetical length of zero. As with the model for tagging data, was the individual asymptotic length of thefish drawn from the random normal distribution . represented the distribution of individual measurement error and was similarly random, drawn from the distribution . Equation 12 describes the log-likelihood function derived from these equations.

An appropriate overall objective likelihood function (E13) was then defined from the sum of the negative log-likelihood functions for tag-recapture, direct aging, and length frequency, each with its own scaling constant, .

*Defining an objective function and estimating integrative growth parameters*

A single set of growth parameters best describing the data was obtained by minimizing the objective likelihood function (E13).

By manipulating the value of scaling constants (), how similar datasets were treated, and which datasets were included, six additional model structures were developed and evaluated (Table 3). Two approaches were used to define the scaling constants within each model’s objective likelihood function. 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 ().

The structure of model 5 fit only tagging data from the OTP study while models 6-11 incorporated the additional length-at-age and length frequency data and 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 *P. filamentosus* (Table 3; Wakefield et al 2017).

The six candidate integrative model structures (Models 6-11) were evaluated against one another using the following repeated training-testing cross validation procedure (Burman 1989) to determine the combination of model weighting, data pooling, and data sources parameter estimates that consistently best predicted observed growth from tagging data. Each model structure was trained using two-thirds of the tagging data (n = 258) selected at random while the remaining one-third (n = 129) was reserved for evaluating each model’s predictive ability. Model performance was evaluated using the parameters and estimated from training data, applied to the length at tagging and time at liberty of each individual in the validation set to predict length at recapture using Equation 2. The variance (between the predicted ( and observed (length of each fish recapture was used as a metric for comparing the performance of competing model structures (E14).

The preferred model structure was the one whose estimated parameters most frequently produced the smallest variance. This procedure was repeated 10,000 times. The preferred model structure was the one that most frequently reported the lowest variance across all of these iterations. To determine if incorporating additional data sources improved predictive performance, cross validation variances for the preferred model structure were compared to those calculated using a model structure identical to Model 5, calculated including only tagging data.

The integrative 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 reconstructed study data. Each study period in the pseudo dataset contained the same number of observations as in the corresponding time time period of the original study data.

***Results***

*Opakapaka Tagging Program*

Of the 4,179 *P. filamentosus* tagged 432 individuals were recaptured at least once (10.3%). 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.

Initial fork length at capture across all individuals ranged in size from 16.51 to 53.34 cm (mean = 31.90 cm, standard deviation (s.d.) = 5.48). For fish that were recaptured later, initial size ranged from 19.1 cm and 52.8 cm (mean = 32.8, s.d. = 5.08). For those fish that were later recaptured, fork length at recapture ranged between 22.9 cm and 76.2 cm (mean = 41.9, s.d. = 8.67). 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 666 days (s.d. = 625).

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 432 fish recaptured, 394 were recaptured a single time, 35 fish were recaptured a total of two times, one fish was recaptured 3 times, and two fish were recaptured 4 times. We alsoWe alsoexcluded from analysis 45 individuals for whom time at liberty was less than 60 days yielding a data set of 387 unique individuals.

*Estimating Growth Parameters from Tagging Data: Bayesian Approach*

The Bayesian hierarchical approach 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. Models 2-4 have higher coefficients of variation for and suggesteding that individual variability in both and was 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 were not credible. Model 1 (preferred) and Model 2 performed similarly suggesting that the primary source of individual variability was due to variability in the growth parameter. Other Bayesian model specifications for Model 1 were calculated (Table 2). 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 4). Bootstrap confidence intervals of parameters and overlapped and parameters from Bayseian models 1 and 2 (Table 1). 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 consistently 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 10,000 cross validation iterations to determine model structure, the mean predictive variance metric ranged between 7.29 and 24.96 (mean = 14.20, s.d. = 2.20) where a lower predictive variance indicates a better model fit. From all candidate models, the structure of Model 11 best predicted cross validation data in 3,486 of 10,000 iterations and its predictive variance ranged between 7.29 and 20.10 (mean = 13.64, s.d. = 1.91). As a result this was determined to be the preffered integrative model structure. The structure of Model 5, fit exclusively using tagging data, ranged in predictive variance between 7.17 and 26.09 (mean = 14.35, sd = 2.44). The structure of Model 11 performed better than the structure of Model 5 in 6351 of 10,000 cross validation iterations. Differences in predictive variance between these two competing structures ranged between -1.60 and 10.80 (mean = 0.72, s.d. = 1.37) and indicated that the inclusion of additional growth data did improve the predictive capability of growth models compared to tagging data alone. Bootstrapped parameter estimates refit using the prefered model structure and Model 5’s tagging only data are summarized in table 1 and reported in full in table 4. When fit to the entire tagging data set, the residual pattern of Model 11 also underestimated lengths at recapture for the largest individuals.

***Discussion***

Bayesian and maximum likelihood fitting methods produced similar growth parameter estimates. The similarity between parameters estimated by Model 1, where individual variability was accounted for in both and terms and Model 2, where was fixed indicate that the primary source of individual variability is the term. These results were consistent with previous studies of growth in other species indicating that models accounting for individual variability in both terms provided the best fit but accounting for individual variation in only the term produces parameter estimates still sufficient to describe growth while significantly reducing the computational complexity required for maximum likelihood estimation. Models 5-11 were evaluated under these parameter assumptions. Model 5 and Model 2 were structurally consistent in their treatment of and and the data used to estimate these parameters. Parameters estimated by Models 1 and 2 were contained within the 95% confidence intervals of Model 5.

The use of tagging data alone in Model 5 resulted in estimates of lower than all previous studies where growth has been fit as a function of age. This is likely due to underrepresentation of the largest size classes in the tagging data resulting in growth curves that asymptote prematurely. The tagging data described here includes *P. filamentosus* with fork lengths at capture spanning 19.1 - 52.8 cm (mean = 32.9, s.d. = 5.08). Using growth parameters estimated in this study, this data corresponds to fish mean ages between 1.5 and 7 years (Figure 5). Incorporating the information of larger individuals (up to 76.8 cm) from length-at-age data resulted in larger estimates of and smaller estimates of . Recent work on *P. filamentosus* otoliths using lead-radium and bomb-radiocarbon dating indicate that *P. filamentosus* can live in excess of 45 years (Andrews et al. 2012). Information from older age classes is very important for grounding the upper end of the growth curve.

Parameter estimates from integrative models inclusive of the largest fish from length-at-age data better predicted growth than those fit with only tagging data in over 60% of cross validation iterations. On this basis, integrative parameters likely provide better estimates for growth of species in the Hawaii region. The candidate integrative model structure that consistently outperformed competing model structures was Model 11. Estimates of and fit using the structure of Model 11 were most similar to those of Ralston and Miyamoto (1983) and Andrews et. al. (2012) with parameter estimates from both of these studies within the confidence intervals obtained (Table 1). Despite concerns surrounding the reliability of the method, both of these studies relied heavily on age data from otolith annuli to derive growth parameters. Despite the similarity between these results, the preferred integrative model structure (Model 11) omitted otolith annuli when estimating growth parameters suggesting that inclusion of validated age data from very large fish is important for obtaining accurate growth estimates using this method.

In addition to ensuring sampling across the whole size range of the species, sexual dimorphism in growth may play a role in the underestimation of length at recapture for the largest fish, both in the present models and in previous studies. Parameters of nearly all growth models, here and previous studies, underestimate the length at recapture for the largest fish in the OTP dataset. It is possible that this is 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. or these fish undergo a dietary shift allotting more energy for growth during the last phase. Sexual dimorphism may also explain the poor predictive ability for individuals reaching the largest sizes. Age-at-length and length frequency data obtained for the species in the Seychelles described 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 et al. 1997). Sex data were not available for fish in this study meaning that growth parameters represent an average across both sexes. If one sex attains a greater asymptotic length than the other, that sex is likely to be over represented in the largest size classes relative to the total population. At sizes where the sex ratio of those individuals is similar to the sex ratio across all sizes of the population, averaging of model parameters results as excess model deviation. However, if the sex ratio of fish attaining the largest sizes is not representative of the sex ratio across all size classes, growth parameters estimated without knowledge of sex will underestimate recapture lengths for largest individuals while overestimating the recapture length of the largest individuals of the opposite sex. Similar residual patterns have been noted for other species with sexually dimorphic growth when parameters are estimated from tagging data without knowledge of sex (Personal Communication, A.F. Holdsworth Hall, 160 Holdsworth Way, Amherst, MA).

Prior estimations of growth parameters for *P. filamentosus* in the Central Pacific region appear to have been determined without consideration of sex and similarly underestimate growth in the largest fish. A method for externally sexing *P. filamentosus* has been recently described but was unknown at the time the data for this study were collected (Luers et al. 2017) and thus all models fit in this study are sex agnostic. Future work to refine growth estimates for *P. filamentosus* should consider the possibility that growth trajectories may differ between males and females.

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 very important for management.

Results presented here synthesize 30+ years of efforts to determine growth for *P. filamentosus* in the Hawaiian Archipelago, including previously unreported tagging data, 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 with broad genetic homogeneity in the species throughout the Hawaiian Archipelago (Shaklee and Samollow 1984, Gaither et al. 2010, 2011).Parameter estimates derived from integrative models that incorporated additional length frequency and length-at-age data were better able to predict growth. These parameters were highly consistent with those derived by radio-isotopic composition of otolith material and counts of otolith microincrements and annuli by Andrews et al. (2012) and those fit only with annuli data without constraining by Ralston and Miyamoto (1983).

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 in this study are consistent with studies that have exclusively utilized a direct aging approach. 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. Improved fit of the models that incorporated larger fish sizes show the importance of adequate sampling. Additionally, we speculate this may be the result of dimorphic growth between sexes, where only one sex attains the largest sizes. Sex 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, hook 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 direct aging 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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**Appendix 1**. WinBUGS code for Bayesian hierarchical growth model. Model 1 incorporates both L∞ and K individual variability; Model 2 incorporates L∞ individual variability; Model 3 incorporates K individual variability; and Model 4 incorporates no individual variability. Methodology from Zhang et al. (2009).

**# Model 1**

**model{**

**for (i in 1:476) {**

**for (j in 2:n[i]) {**

**L[i, j] ~ dnorm(L\_Exp[i, j], tau)**

**L\_Exp[i, j] <- Linf[i] \*(1.0 - exp(-k[i]\*(A[i]+t[i, j -1])))**

**L.pred[i, j] ~ dnorm(L\_Exp[i, j], tau)**

**p.value[i, j] <- step(L.pred[i, j] - L[i, j])**

**}**

**L[i, 1] ~ dnorm(L\_Exp[i, 1], tau)**

**L\_Exp[i, 1] <- Linf[i] \*(1.0 - exp(-k[i]\*A[i]))**

**L.pred[i, 1] ~ dnorm(L\_Exp[i, 1], tau)**

**p.value[i, 1] <- step(L.pred[i, 1]- L[i, 1])**

**Linf[i] ~ dnorm(Linf\_mu, Linf\_tau)**

**k[i] ~ dnorm(k\_mu, k\_tau) I(0,1)**

**A[i] ~ dgamma(shape, rate)**

**}**

**Linf\_std <- sqrt(1/Linf\_tau)**

**k\_std <- sqrt(1/k\_tau)**

**var <- 1/tau**

**Linf\_mu ~ dnorm(100, 0.0001)**

**Linf\_tau ~ dgamma(0.001, 0.0001)**

**shape ~ dunif(0, 100)**

**rate ~ dunif(0, 100)**

**k\_mu ~ dbeta(1, 1)**

**k\_tau ~ dgamma(0.001, 0.0001)**

**tau ~ dgamma(0.001, 0.0001)**

**}**

**# Model 2**

**model{**

**for (i in 1:476) {**

**for (j in 2:n[i]) {**

**L[i, j] ~ dnorm(L\_Exp[i, j], tau)**

**L\_Exp[i, j] <- Linf[i] \*(1.0 - exp(-k\*(A[i]+t[i, j -1])))**

**L.pred[i, j] ~ dnorm(L\_Exp[i, j], tau)**

**p.value[i, j] <- step(L.pred[i, j] - L[i, j])**

**}**

**L[i, 1] ~ dnorm(L\_Exp[i, 1], tau)**

**L\_Exp[i, 1] <- Linf[i] \*(1.0 - exp(-k\*A[i]))**

**L.pred[i, 1] ~ dnorm(L\_Exp[i, 1], tau)**

**p.value[i, 1] <- step(L.pred[i, 1]- L[i, 1])**

**Linf[i] ~ dnorm(Linf\_mu, Linf\_tau)**

**A[i] ~ dgamma(shape, rate)**

**}**

**Linf\_std <- sqrt(1/Linf\_tau)**

**k\_std <- sqrt(1/k\_tau)**

**var <- 1/tau**

**k ~ dnorm(k\_mu, k\_tau) I(0,1)**

**Linf\_mu ~ dnorm(100, 0.0001)**

**Linf\_tau ~ dgamma(0.001, 0.0001)**

**shape ~ dunif(0, 100)**

**rate ~ dunif(0, 100)**

**k\_mu ~ dbeta(1, 1)**

**k\_tau ~ dgamma(0.001, 0.0001)**

**tau ~ dgamma(0.001, 0.0001)**

**}**

**# Model 3**

**model{**

**for (i in 1:476) {**

**for (j in 2:n[i]) {**

**L[i, j] ~ dnorm(L\_Exp[i, j], tau)**

**L\_Exp[i, j] <- Linf\*(1.0 - exp(-k[i]\*(A[i]+t[i, j -1])))**

**L.pred[i, j] ~ dnorm(L\_Exp[i, j], tau)**

**p.value[i, j] <- step(L.pred[i, j] - L[i, j])**

**}**

**L[i, 1] ~ dnorm(L\_Exp[i, 1], tau)**

**L\_Exp[i, 1] <- Linf \*(1.0 - exp(-k[i]\*A[i]))**

**L.pred[i, 1] ~ dnorm(L\_Exp[i, 1], tau)**

**p.value[i, 1] <- step(L.pred[i, 1]- L[i, 1])**

**k[i] ~ dnorm(k\_mu, k\_tau) I(0,1)**

**A[i] ~ dgamma(shape, rate)**

**}**

**Linf\_std <- sqrt(1/Linf\_tau)**

**k\_std <- sqrt(1/k\_tau)**

**var <- 1/tau**

**Linf ~ dnorm(Linf\_mu, Linf\_tau)**

**Linf\_mu ~ dnorm(100, 0.0001)**

**Linf\_tau ~ dgamma(0.001, 0.0001)**

**shape ~ dunif(0, 100)**

**rate ~ dunif(0, 100)**

**k\_mu ~ dbeta(1, 1)**

**k\_tau ~ dgamma(0.001, 0.0001)**

**tau ~ dgamma(0.001, 0.0001)**

**}**

**# Model 4**

**model{**

**for (i in 1:476) {**

**for (j in 2:n[i]) {**

**L[i, j] ~ dnorm(L\_Exp[i, j], tau)**

**L\_Exp[i, j] <- Linf\*(1.0 - exp(-k\*(A[i]+t[i, j -1])))**

**L.pred[i, j] ~ dnorm(L\_Exp[i, j], tau)**

**p.value[i, j] <- step(L.pred[i, j] - L[i, j])**

**}**

**L[i, 1] ~ dnorm(L\_Exp[i, 1], tau)**

**L\_Exp[i, 1] <- Linf \*(1.0 - exp(-k\*A[i]))**

**L.pred[i, 1] ~ dnorm(L\_Exp[i, 1], tau)**

**p.value[i, 1] <- step(L.pred[i, 1]- L[i, 1])**

**A[i] ~ dgamma(shape, rate)**

**}**

**Linf\_std <- sqrt(1/Linf\_tau)**

**k\_std <- sqrt(1/k\_tau)**

**var <- 1/tau**

**k ~ dnorm(k\_mu, k\_tau) I(0,1)**

**Linf ~ dnorm(Linf\_mu, Linf\_tau)**

**Linf\_mu ~ dnorm(100, 0.0001)**

**Linf\_tau ~ dgamma(0.001, 0.0001)**

**shape ~ dunif(0, 100)**

**rate ~ dunif(0, 100)**

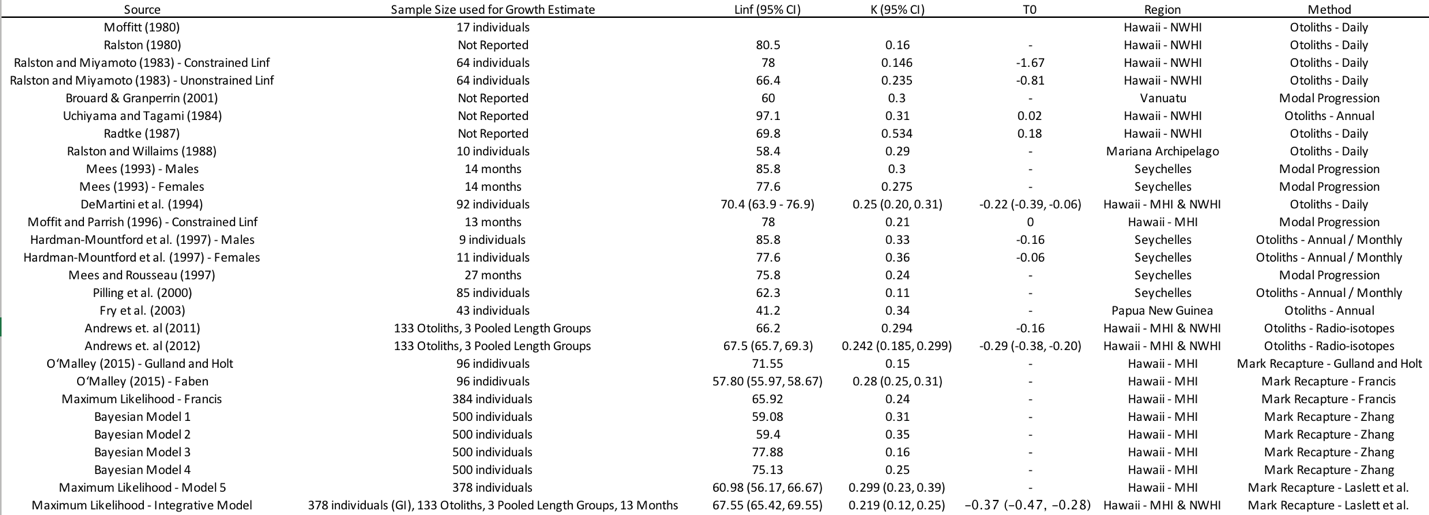
**k\_mu ~ dbeta(1, 1)**

**k\_tau ~ dgamma(0.001, 0.0001)**

**tau ~ dgamma(0.001, 0.0001)**

**}**

**Table 1.** Growth parameters for *P. filamentosus* estimated both in Hawaii and from studies elsewhere in the Indo-Pacific region. When available in the literature, 95% confidence intervals for parameter estimates are presented in brackets next to parameter point estimates. The column “Sample Size Used for Growth Estimates” refers to the number of unique data points used to estimate growth parameters.



**Table 2**. Bayesian hierarchical growth model specifications for Model 1 incorporating both K and L∞ individual variability. Monte Carlo simulation was burned in for n=10,000 runs with every 50th of the following 500,000 runs retained for tabulation into the posterior distributions. Variable names are kept consistent with the Appendix 1 WinBUGS code and are not consistent with text references to von Bertalanffy growth parameters but remain intuitively similar (e.g., K=k\_mu, L∞=Linf\_mu).



**Table 3.** A reference for the candidate model structures used to determine the preferred integrative model structure.

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Model Structure ID** | **Growth Increment** Mark Recapture  OTP | **Direct Aging** Integrated Otolith Annuli  Ralston & Miyamoto (1983) | **Direct Aging** Otolith Microincrements  Demartini et al. (1994) | **Direct Aging** Bomb Carbon  Andrews et al. (2012) | **Direct Aging** Lead:Radium  Andrews et al. (2012) | **Length Frequency** Modal Progression  Moffitt & Parrish (1996) | **Weighting** | **Pooled Within Data Types?** |
| **Model 6** | X |  |  |  |  |  | NA | NA |
| **Model 7** | X | X | X | X | X | X | Equal | Yes |
| **Model 8** | X | X | X | X | X | X | By n | Yes |
| **Model 9** | X | X | X | X | X | X | Equal | No |
| **Model 10** | X | X | X | X | X | X | By n | No |
| **Model 11** | X |  | X | X | X | X | Equal | No |
| **Model 12** | X |  | X | X | X | X | by n | No |

**Table 4.** Sample and population parameter estimates from maximum likelihood growth estimates for Model 5 (OTP tagging data only) and the Model 11 (preferred integrative model). For both models, parameter estimates fit to the full data set are reported in the Sample Estimate columns while bootstrapped parameter estimates (Median, 2.5%, 97.5%) are reported under the Population CI column.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | **Model 5** | | **Model 11** | |
| **Parameter** | **Sample Estimate** | **Population Estimate** | **Sample Estimate** | **Population Estimate** |
|  | 60.92 | 60.98 (56.17, 66.67) | 68.52 | 67.55 (65.42, 69.55) |
|  | 5.32 | 5.3 (4.53, 6.07) | 4.22 | 5 (4.26, 5.68) |
|  | 0.300 | 0.299 (0.229, 0.393) | 0.173 | 0.219 (0.198, 0.245) |
|  | 0.95 | 0.95 (0.8, 1.09) | 1.34 | 1.11 (1.03, 1.19) |
|  | 0.19 | 0.19 (0.15, 0.24) | 0.16 | 0.17 (0.14, 0.2) |
|  | 2.10 | 2.08 (1.5, 2.55) | 2.9 | 2.39 (2, 2.77) |
|  | - | - | -0.63 | -0.37 (-0.47, -0.28) |
|  | - | - | 1.40 | 0.96 (0.49, 1.31) |
|  | - | - | 3.09 | 4.63 (4.15, 5.15) |

**Figure 1.** The length of *P. filamentosus* recaptured and included in analysis of OTP tagging data and the distribution of times at liberty. The fork length of fish during tagging is highlighted in red while length at recapture is shown in blue.



**Figure 2:** Coefficient of variation for 2 von Bertalanffy growth curve parameters K and L∞ for *P. filamentosus*. Individual variability was examined incorporating individual variability in both parameters, in either one of the parameters in series, or in neither parameter.



**Figure 3.** Plots comparing observed and predicted recapture lengths fit using parameter point estimates from Bayesian Models 1 and 2, as well as Maximum likelihood Models 5 and 11. Length at recapture was predicted as a function of length at marking and time at liberty. The 1:1 line indicates where points would fall if model parameters perfectly predicted length at recapture.



**Figure 4.** Residual plots showing deviation from model predictions as a function of an individual’s length at marking for Bayesian Models 1 and 2, as well as Maximum likelihood Models 5 and 11. These plots were visually inspected to determine residual trends.



**Figure 5.** Comparison of von Bertalanffy growth function curves produced from parameters during this study. Horizontal dashed lines indicate the minimum and maximum length of individuals at the time of marking recorded in the OTP dataset.

