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Abstract: *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 initiated a fisher participation mark-recapture study to quantify growth and other life history parameters for the species. Over a span of approximately 10 years, 10.5% of 4,179 tagged fish were recaptured. We compared Bayesian and maximum likelihood approaches to estimate von Bertalanffy growth parameters from the tagging data. Direct aging and length frequency data previously used in other published regional growth studies were incorporated to produce integrated estimates of growth. Results from our preferred integrated model reconcile 30+ years of effort from various methods to estimate growth parameters ($L_{\infty} = 67.6$ cm FL and $K = 0.22$) and demonstrate the importance of individual variability in *P. filamentosus* due primarily to the asymptotic length parameter L_{∞} . 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.

Dear Editors and Reviewers,

We are excited to submit for your consideration a manuscript entitled "Comparing age and growth estimates from Bayesian and integrative data approaches for the deepwater snapper *Pristipomoides filamentosus* in the Hawaiian Islands". We hope that this manuscript provides a valuable contribution as a *Research Paper*.

Deep-water snappers are an important resource throughout the Indo-Pacific. These species are particularly susceptible to overfishing due to their longevity, delayed maturity, and slow growth. *Pristipomoides filamentosus* is a key component of Hawaii's deep-water bottomfish complex, accounting for over half of the revenue of the region's commercial bottomfish fishery.

Starting in the 1980s, a great deal of effort has been put forth to understand how these fish grow for the purpose of assessment and management. In this manuscript, we report growth parameters estimated using a previously unpublished mark-recapture dataset using Bayesian and maximum likelihood methods. These estimates are fit with nearly four times as many observations as those previously reported. In addition to reporting these growth estimates, we also report estimates obtained using models that incorporate six additional data sources from four prior studies to produce integrative growth estimates. The integrative parameters better predict growth observed in recaptured fishes than those fit using tagging data exclusively. They also better predict observed growth than growth estimates from previous studies.

Growth is a key life history parameter often used directly or indirectly in the management process. By refining estimates for *P. filamentosus* in Hawaii, our integrative estimates can improve assessment models for this species.

Please contact us if you require further information, and we look forward to hearing from you.

Sincerely,

A handwritten signature in black ink, appearing to be 'S. Scherrer', with a long, sweeping horizontal line extending to the right.

Stephen R. Scherrer

Comparing age and growth estimates from Bayesian and integrative data approaches for the deepwater snapper *Pristipomoides filamentosus* in the Hawaiian Islands

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Highlights

- Growth parameters were estimated for *P. filamentosus* using Bayesian and integrative maximum likelihood methods.
- The best parameters were $L_{\infty} = 67.6$ cm FL, $k = 0.22$, $t_o = -0.37$ yr.
- These estimates support those derived from using radioisotopic analysis of bomb-carbon.
- Growth parameters estimated with length-at-age, length-frequency, and growth-increment data consistently outperform estimates from any single method.
- Negatively biased growth predictions for the largest individuals suggests the potential for sexually dimorphic growth.

Abstract

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 initiated a fisher participation mark-recapture study to quantify growth and other life history parameters for the species. Over a span of approximately 10 years, 10.5% of 4,179 tagged fish were recaptured. We compared Bayesian and maximum likelihood approaches to estimate von Bertalanffy growth parameters from the tagging data. Direct aging and length frequency data previously used in other published regional growth studies were incorporated to produce integrated estimates of growth. Results from our preferred integrated model reconcile 30+ years of effort from various methods to estimate growth parameters ($L_{\infty} = 67.6$ cm FL and $K = 0.22$) and demonstrate the importance of individual variability in *P. filamentosus* due primarily to the asymptotic length parameter L_{∞} . 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.

1. Introduction

Pristipomoides filamentosus (Valenciennes, 1830) is a species of long-lived deep-water snapper distributed throughout the tropical Pacific and Indian Oceans (Allen, 1985; Gaither et al., 2011). Known as opakapaka in Hawaii, the species constitutes a significant fraction of the region's commercial bottomfish fishery (Ralston and Polovina 1982, Langseth et al. 2018). The current stock assessment for this fishery used a surplus production model fit for the 6 species of snapper and one endemic grouper (Langseth et al., 2018). However there is interest in the potential use of species-specific, age-structured assessments for this fishery which require accurate life history studies of age and growth (Langseth et al., 2018; Mauder et al., 2015).

In Hawaii and elsewhere in the Indo-Pacific, growth parameters have been estimated for *P. filamentosus* using a variety of methods (Table 2). Direct aging approaches using length-at-age data from otolith growth increments have been used to derive growth parameters for *P. filamentosus* (Ralston & Miyamoto, 1983; Uchiyama & Tagami, 1984; Radtke, 1987; DeMartini, Landgraf & Ralston, 1994, Ralston & Williams, 1988). However, this method relies on the integration of daily otolith bands 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). A length frequency study focused on early growth in juvenile fish but individual variability was not considered when extrapolating growth for larger size classes which can result in biased parameter estimates (Moffitt and Parrish, 1996; Sainsbury, 1980). An ongoing mark-recapture study has attempted to estimate growth parameters using a growth increment approach but preliminary results have been limited by the size distribution of recaptured individuals and use model parameterizations incompatible with other methods for determining growth (R. I. C. C. Francis, 1988; O'Malley, 2015). While the methods of the aforementioned studies produced individual estimates of growth parameters, none of them holistically integrated across the three classes of data (direct aging, modal progression, growth increment) 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 (Eveson et al., 2004; R. I.C.C. Francis, 1988; Wang et al., 1995). Structural modifications to Fabens (1965) parameterization of the von Bertalanffy growth model address issues of compatibility between growth parameters derived from tagging studies and other methods (Maller and Deboer 1988, James 1991, Palmer et al.

1991, Laslett et al. 2002, Eveson et al. 2004, 2007, Zhang et al. 2009). Maximum likelihood and Bayesian model fitting procedures accommodate individual variability by describing population parameters using probability distributions (R. I.C.C. Francis, 1988; Kimura et al., 1993; Wang et al., 1995; Zhang et al., 2009). Bayesian approaches allow K and L_{∞} to be sampled in this manner and can account for prior information when estimating parameters (Zhang et al. 2009). Maximum likelihood approaches typically treat K 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).

Here we derive growth parameters using Bayesian and maximum likelihood methods applied to a previously unreported tagging data of *P. filamentosus* marked and recaptured in the Main Hawaiian Islands (MHI). Parameters estimated from the tagging data using a Bayesian framework are compared to estimates integrating tagging data with previous length-at-age and length frequency data collected from the MHI and Northwestern Hawaiian Islands (NWHI) derived through maximum likelihood. We then compare these new growth estimates to those previously reported for *P. filamentosus* the Hawaiian Archipelago.

2. Materials and Methods

2.1 Opakapaka Tagging Program

Tagging data used for this analysis were 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 1993 the Opakapaka Tagging Program (OTP), led by staff biologist

Henry Okamoto and operating from fishing vessels contracted out of Honolulu Harbor, tagging and releasing 4,179 *P. filamentosus* in total.

All tagging occurred in the Main Hawaiian Islands (MHI). Coarse location data was provided by the commercial statistical reporting grid areas in a given fish was tagged and recaptured (Table 1, Figure 1). Effort was concentrated primarily around the island of Oahu and the Maui Nui complex consisting of the islands of Maui, Molokai, Lanai and Kahoolawe. Since 1990, these areas have accounted for approximately 67.7% of Hawaii's commercial bottomfish harvest. Less than 1% of fish in this study were tagged off the islands of Niihau or Hawaii (Big Island).

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 assess survival likelihood. Fish appearing lively and upright were deemed likely to survive and thus suitable candidates for tagging. If the stomach was inverted and full of gas, it was punctured using a small sharp instrument (e.g., scalpel, hypodermic needle, fishhook). A few scales were carefully removed and a small (~1 cm) incision was made near the fish's anal opening to assist in expelling gas from the body cavity. Fish were then 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, as well as the location and time of capture were recorded before the fish was returned headfirst to sea with downward momentum to assist in counteracting buoyancy caused by any residual gas.

Reports of recaptured *P. filamentosus* were reported up to a decade after they were tagged, most recently in October of 2003 (Kobayashi et al., 2008; Okamoto, 1993). There were 487 recaptures recorded for 439 unique individuals for a recapture rate of 10.5% of tagged fish.

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. Tagged fish recaptured by OTP personnel were fit with an additional tag and released again.

2.2 Tagging Data Management

The data collected by OTP was entered into a spreadsheet with subsequent analysis performed using R (R Core Team, 2014), the Bayesian statistical software JAGS (Plummer, 2003), and the R package R2Jags (Su and Yajima, 2012). 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 linearly transformed from inches to centimeters prior to model fitting. Observed growth (Δl) and time at liberty (Δt) were calculated for each fish. If an individual was recaptured on more than one occasion, Δl and Δt were only calculated between the first marking event and the last recapture so as to not violate assumptions of independence. Fish with Δt less than 60 days were excluded from the dataset.

2.3 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 predicted length of a captured individual is expressed as:

$$(E1) \ L_{i,j} = L_{\infty,i}(1 - e^{-K_i(A_i+t_{i,i})})$$

This is parameterized such that $L_{i,j}$ is the length of individual i for the j th time the individual is captured, $t_{i,j}$ is the time-at-liberty for individual i for the j th capture, A_i is the relative age of individual i at tagging (age minus t_0), and K_i and $L_{\infty,i}$ are the von Bertalanffy growth parameters for the i th individual. These individual parameters were drawn from Gaussian distributions defining the population means for K and L_{∞} . Uninformative priors were used for all input parameters, using Gaussian, gamma, beta, and uniform distributions following the approach of Zhang et al. (2009). The JAGS code for specifying these parameters and performing this analysis is provided in Appendix 1.

The model which allowed both the K and L_{∞} parameters to vary across individuals as described above is henceforth referred to as Model 1. Three additional models were run with various constraints to K and L_{∞} . Model 2 used a fixed K parameter while allowing the L_{∞} parameter to vary across individuals. 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 3 used a fixed L_{∞} parameter while allowing the K parameter to vary across individuals and both parameters were fixed under Model 4. Model 4 would *a priori* be most similar to the Fabens approach, with both fixed K and L_{∞} , but with the added feature of estimating ages at initial tagging, A_i . It is the inclusion of this term that models growth as a function of age, rather than length, which allows for direct comparison between parameters estimated using tagging data and those obtained from direct-age and length frequency approaches (Wang et al., 1995).

Evaluating the restrictive assumptions of models 2-4 was accomplished by comparing growth parameters to those estimated by Model 1. Model 1 is the presumptive best estimate for *P. filamentosus* von Bertalanffy growth curve parameters, since it allows the most flexible incorporation of individual variability in the parameter estimation process. If a given parameter is relatively stable when the parameter was allowed to be variable across individuals and when it was treated as fixed for the population, then it might be inferred that treating this parameter on an individual basis is not warranted. However, if parameter estimates differed when the parameter was fixed, then it might be inferred that treating this parameter on an individual basis is necessary.

For each Bayesian hierarchical model run, the first 150,000 samples from the posterior distribution were treated as burn-in and discarded from the Monte Carlo simulation. Every 50th sample from the following 1,400,000 samples (number kept = 28,000) was tabulated into the posterior distributions to reduce potential autocorrelation between sequential values or strings of values. The mean K and L_{∞} values from the posterior distribution were used as metrics of population mean values. Median values deviated from mean values by less than one half of 1 percent (Table 3), indicative of symmetrical distributions easily characterized by any descriptor of value tendency (i.e., mean, median, or mode). Initial starting estimates of K and L_{∞} were obtained by fitting Fabens (1965) approach using non-linear least squares (Table 2). Two additional chains were run simultaneously with initial starting values 50% lower and 100% higher than the Fabens' estimates. This resulted in nearly identical solutions as shown in Table 3. Convergence was also ascertained by examination of the Gelman-Rubin statistic (Gelman and Rubin, 1992).

The fit of each model was assessed by calculating its Bayesian p-value from the posterior predictive distribution and comparing DIC values for each model. Bayesian p-values were simulated using the model's posterior distribution and test whether simulated data is more extreme than the observed data. Bayesian P-values range between 0 and 1 where values approaching 0.5 indicate the model is a good fit to the data, while extreme values near 0 or 1 indicate that the model does not adequately represent the data (Meng, 1994).

2.4 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.

$$(E2) \quad l_{ij} = \mu_{\infty}(1 - e^{-K(a_i + \Delta t_i)}) + \varepsilon_{ij}$$

This method derived growth parameters from the 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, L_{∞} , is treated as a normal random effect $N(\mu_{\infty}, \sigma_{\infty}^2)$ while K is treated as a fixed unknown parameter. The distribution of L_{∞} is assumed to be normal with a mean μ_{∞} and standard deviation σ_{∞}^2 , accounting for differences between an individual the total population. Rather than using length increments to fit observed growth, a bivariate normal joint distribution of lengths recorded at marking and recapture was is to estimate each individual's age at tagging a_i . The distribution of individual a_i s is A and is treated as a random effect with a lognormal distribution $L(\mu_{\log A}, \sigma_{\log A}^2)$. Measurement error was also treated as a random normal distribution $N(0, \sigma^2)$. An unconditional joint density was then derived for each individual by integrating their individual joint distribution with respect to a . 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 cost function obtained by summing the unconditional joint density $h(l_1, l_2)$ of each individual (E3).

$$(E3) -\ln(\lambda_1) = - \sum_i \ln h(l_{m,i}, l_{r,i})$$

This approach was used to estimate values of the parameters μ_∞ , σ_∞^2 , K , $\mu_{\log A}$, $\sigma_{\log A}^2$, and σ^2 . Two-sided 95% confidence intervals (2.5%, Median, 97.5%) for each parameter were then estimated from 10,000 successful bootstrap iterations. During each iteration, the model was refit using data randomly resampled from the original tagging data with replacement.

2.5 Estimation of Integrative Growth Parameters using sources of growth data

Datasets previously used to estimate regional growth for *P. filamentosus* in the MHI and NWHI and our tagging data exclusively from the MHI 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). Additional datasets that were included represent both direct aging and length frequency approaches and are briefly described.

2.6 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 in the original study reports 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 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 assuming the mean of each distribution corresponded to the observed mode. A bimodal Gaussian mixture model was fit for the data collected between the months of October-February, as the original study reported that two cohorts were present during this period. A single cohort was present the remainder of the year. The estimated mean fork length, $\hat{\mu}_{ijk}$, and standard error, s_{ijk} , of each cohort during each sampling period was used to estimate growth parameters (E4).

$$(E4) \quad \hat{\mu}_{ijk} = \mu_{\infty} \left(1 - e^{-K(a_{ijk} - a_0)} \right) + e_{ijk} + \varepsilon_{ijk}$$

With this model, i, j , and k reflect the fishing year, month, and age cohort, respectively. The estimated age of each cohort during a sampling period is denoted by a_{ijk} . Ages were estimated relative to the month of July when peak spawning of *P. filamentosus* occurs (Luers et al., 2017). This produced age estimates between 3 and 19 months. Sampling and residual model errors were described using random normal distributions $e_{ijk} \sim N(0, s_{ijk}^2)$ and $\varepsilon_{ijk} \sim N(0, \sigma_{\varepsilon}^2)$ respectively. In contrast to tagging and direct aging methods, length frequency approaches lack the information to estimate the variance component of asymptotic length (L_{∞}), so this term was modeled as fixed effect, μ_{∞} . From this, the expected mode fork length of each cohort (E6), and associated variability during each sampling period (E7) were used to minimize the model's

negative log-likelihood cost function (E8). The rationale for these approximations is discussed to greater depth in Eveson et al. 2004.

$$(E6) \quad E(\hat{\mu}_{ijk}) = \mu_{\infty} (1 - e^{-K(a_{ijk} - a_0)})$$

$$(E7) \quad V(\hat{\mu}_{ijk}) = s_{ijk}^2 + \sigma_{\varepsilon}^2$$

$$(E8) \quad -\ln(\lambda_2) = \frac{1}{2} \sum_i \sum_j \sum_k \left[\ln(2\pi V(\hat{\mu}_{ijk})) + \frac{(\hat{\mu}_{ijk} - E(\hat{\mu}_{ijk}))^2}{V(\hat{\mu}_{ijk})} \right]$$

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227 *2.7 Parameter Estimation: Direct Aging Data*

Sources of direct ageing data included four length-at-age datasets from three prior growth studies. Each dataset estimated age differently. Methods for estimating age included analytical integration of otolith bands (Ralston and Miyamoto, 1983, n = 65), counts of otolith micro increments (DeMartini et al., 1994, n = 35), comparison of otolith derived bomb radiocarbon ratios ($\Delta^{14}\text{C}$) relative to a standard reference obtained from hermatypic coral cores from the Hawaiian Archipelago (Andrews et al., 2012, n = 33), and otolith derived lead-radium ratios pooled by size class (Andrews et al., 2012, n = 3).

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

$$(E9) \quad l_i = l_{\infty i} (1 - e^{-K(a_i - a_0)}) + \gamma_i$$

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

$$(E10) \quad E(l_i) = \mu_{\infty} (1 - e^{-K(a_i - a_0)})$$

$$(E11) \quad V(l_i) = \sigma_{\infty}^2 (1 - e^{-K(a_i - a_0)})^2 + \sigma_{\gamma}^2$$

Where l_i denotes the length of the i^{th} fish, at age a_i and a_0 was a fixed parameter analogous to t_0 when a fish has a hypothetical length of zero. As with the model for tagging data, $l_{\infty i}$ is the individual asymptotic length of the i^{th} fish drawn from the random normal distribution $L_{\infty} = N(\mu_{\infty}, \sigma_{\infty})$. γ_i represents the distribution of individual measurement error and is similarly random, drawn from the distribution $\gamma = N(0, \sigma_{\gamma})$. Equation 12 describes the log-likelihood cost function derived from these equations.

$$(E12) \quad -\ln(\lambda_2) = \frac{1}{2} \sum_i \left[\ln(2\pi V(l_i)) + \frac{(l_i - E(l_i))^2}{V(l_i)} \right]$$

2.8 Defining an objective cost function and estimating integrative growth parameters

To derive integrated growth parameters across tag-recapture, direct aging, length frequency, and growth increment data sources, an appropriate overall likelihood cost function (E13) is defined from the sum of the negative log-likelihood cost functions for each source, each with their own scaling constant, β . The single set of growth parameters best describing all data sources is obtained through minimization of the overall likelihood cost function, Λ (E13).

$$(E13) \quad \Lambda = \beta_1 \ln(\lambda_1) + \beta_2 \ln(\lambda_2) + \beta_3 \ln(\lambda_3) \dots + \beta_n \ln(\lambda_n)$$

By manipulating the value of scaling constants, how similar datasets were treated, and which datasets were included, six additional model structures for estimating growth in *P. filamentosus* were developed and evaluated (Table 4). Two approaches were used to define the scaling constants (β) within each model structures overall cost function. The first weighted β scaling constants for every data source so that each source had equal influence on the resulting parameter estimates. This was achieved by setting the β constant for each data source equal to the inverse of the number of observations for the data. The second approach weighed β for each

data source relative to the number of observations of within the data set ($\beta_1 = \beta_2 = \beta_3$). This meant that data sources with more observations had a greater influence during parameter estimation.

The structure of model 5 fit only tagging data from the OTP study. The remaining models 6-11 incorporated the additional length-at-age and length frequency data sources and differed in their treatment of β coefficients. Other differences between these models included whether the four direct aging data sources were considered independently and assigned their own log-likelihood cost function or if the four data sources were pooled with a single log-likelihood cost function. Omission of direct aging data where ages were estimated by integrating daily growth increments was also considered as this method is likely to underestimate age (Table 4; Wakefield et al 2017).

The six candidate integrative model structures (Models 6-11) were evaluated against one another using a repeated train-test cross validation procedure (Burman, 1989) to determine the combination of model weighting, data pooling, and data sources parameter estimates that consistently best predicted the growth observed in the tagging dataset. 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 testing model performance. Model performance was evaluated by calculating the mean sum of squared residuals (mssr) using the test dataset. Length at recapture was compared between predictions for the test data made using parameters fit with the training data using Equation 2 and observed length reported in the test set (E14).

$$(E14) \quad s^2 = \frac{1}{n} \sum (L_{ri} - \widehat{L}_{ri})^2$$

The preferred model structure was the one whose estimated parameters most frequently resulted in the lowest mssr over 10,000 iterations. To determine if incorporating additional data sources

improved predictive performance, mssr 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-datasets 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-dataset 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 period of the original study data.

3. Results

3.1 Opakapaka Tagging Program

Of the 4,179 *P. filamentosus* tagged 439 individuals were recaptured at least once (10.5%, Table 1). 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 16.5 to 53.3 cm (mean = 31.9 cm, standard deviation (s.d.) = 5.5) and ranged from 19.1 cm and 52.8 cm (mean = 32.8, s.d. = 5.1) for fish that were later recaptured. 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. = 8.7). 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 2). The mean time at liberty was 1.82 years or 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, 351 were recaptured a single time, 33 fish were recaptured a total of two times, one fish recaptured 3 times, and two fish were recaptured 4 times. We also excluded from analysis 45 individuals for whom time at liberty was less than 60 days yielding a data set of 387 unique individuals.

3.2 Estimating Growth Parameters from Tagging Data: Bayesian Approach

The Bayesian hierarchical approach using the JAGS software yielded mean estimates of L_{∞} and K for each of the Models 1–4 examined (Table 2). Model 1, which incorporated individual variability in both L_{∞} and K yielded mean parameter estimates of $L_{\infty} = 59.9$ cm (coefficient of variation [c.v.] = 2.59) and $K = 0.32$ (c.v. = 8.57). L_{∞} and K parameter estimates for Model 2, where K was fixed, were 60.1 cm (c.v. = 2.74) and 0.35 (c.v. = 45.7) respectively. Under Model 3, where L_{∞} was fixed and K was fit freely $L_{\infty} = 76.9$ cm (c.v. = 42.2) and $K = 0.17$ (c.v. = 8.62) and $L_{\infty} = 77.3$ cm (c.v. = 43.1) and $K = 0.24$ (c.v. = 73.1) for Model 4, where both parameters were fixed. Additional parameters for each of the four models are presented in Table 3. 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. All 4 models appeared to fit the the data well; the mean Bayesian P-values from all retained posterior samples for all models ranged between 0.500 and 0.501. Model 1 had the largest DIC score (10582.86) followed by model 2 (10490.96), model 3 (5033.42), and model 4 (4874.83), however treating model parameters as fixed under models 2-4 resulted in excessively large coefficients of variation suggesting that individual variability in L_{∞} and K is important, with perhaps variability in L_{∞} being more important based upon the response of L_{∞} standard deviation from the base case of Model 1 to the constrained individual variability in Model 3 and Model 4 (Figure 3).

3.3 Parameter estimation using maximum likelihood

The maximum likelihood approach used for Model 5 successfully converged to produce estimates of μ_{∞} , σ_{∞}^2 , K , $\mu_{\log A}$, $\sigma_{\log A}^2$, and σ^2 (Table 5). Bootstrap confidence intervals of parameters μ_{∞} and K overlapped L_{∞} and K parameters from Bayesian models 1 and 2 (Table 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 consistently for all but the largest fish. For fish with recapture lengths exceeding 60 cm, growth models underestimated observed recapture lengths (Figures 3).

3.4 Comparing model performance

Across all 10,000 cross validation iterations to determine model structure, mssr 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 likelihood models, the structure of Model 11 best predicted growth observed in the test data for 3,486 of 10,000 cross validation iterations. The mssr for Model 11 ranged between 7.29 and 20.10 (mean = 13.64, s.d. = 1.91). The structure of Model 5, fit exclusively using tagging data, ranged in predictive variance between 7.17 and 26.09 (mean = 14.35, s.d. = 2.44). The structure of Model 11 performed better than the structure of Model 5 in 6,351 of 10,000 cross validation iterations. Differences in mssr 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 improved the predictive capability of growth models compared to tagging data alone. Bootstrapped parameter estimates refit to the structure of the preferred model (Model 11) and Model 5's tagging only data are summarized in Table 2 and all parameters for models 5-11 are reported in full in Table 5. When fit to the entire tagging data set, the residual pattern of Model 11 underestimated lengths at recapture length for the largest individuals.

4. Discussion

Our integrative model results reconcile 30+ years of efforts to determine growth for *P. filamentosus* in the Hawaiian Archipelago and provides robust support for some observed life history parameters. Growth parameters derived using integrative models that incorporated additional length frequency and length-at-age data were better able to predict observed growth in recaptured fish. These parameters were in agreement with those derived from; 1) the fit of only integrated daily growth increments from otoliths collected in the NWHI without constraining L_{∞} (Ralston and Miyamoto, 1983), 2) integrated daily growth increments and microincrement counts (DeMartini et al. 1994), and 3) the radioisotopic composition of otolith material and

counts of otolith increments from the MHI and NWHI (Andrews et al. 2012) and support the implicit assumption that tagging individuals did not disrupt their growth trajectory. Integrative parameters differed from estimates from an ongoing mark recapture study in the MHI which reported faster growth and smaller asymptotic lengths (O'Malley, 2015). These differences could arise from real changes in growth rate between the periods fish were collected, methodological differences in model interpretation, and/or that thus far, none of the fish recaptured during the ongoing study have been of the largest size classes (maximum size reported = 47.6 cm FL).

Compared to their broader distribution, *P. filamentosus* from the Hawaiian archipelago were generally slower growing but obtained a larger asymptotic length than those from the Mariana Archipelago (Ralston and Williams, 1988) and Papua New Guinea (Fry et al. 2006, Andrews et al. 2012) but were faster growing and smaller in their asymptotic length when compared to estimates from the Seychelles (Hardman-Mountford et al., 1997; Mees, 1993; Mees and Rousseau, 1997; Pilling, 2000).

Of the Bayesian models, Model 1 was presumed optimal because it incorporated individual variability in both L_{∞} and K parameters. Models 2-4 suggest that individual variability in both K and L_{∞} is important, with perhaps variability in L_{∞} being more important based upon the response of L_{∞} standard deviation from the base case of Model 1 to the constrained individual variability in Model 3 and Model 4 (Figure 3). While Models 3 and 4 had lower DIC values, based upon parameter estimates and patterns of standard deviation, it is likely that these models were not credible. Similar parameter estimates obtained from Models 1 and 2 suggested that the primary source of individual variability was due to variability in the L_{∞} parameter. This is consistent with other studies where the best models accounted for individual variability in both terms but accounting for individual variation in the L_{∞} term alone was

sufficient to describe growth while significantly reducing computational complexity (Eveson et al. 2007, Zhang et al. 2009).

Comparing growth parameter estimates fit exclusively with tagging data indicate that Bayesian and maximum likelihood fitting methods performed similarly. The treatment of individual variability in parameters for Model 2 were identical to those used to fit Model 5 (OTP data only). Parameter estimates for Models 1 and 2 were contained within the 95% confidence intervals of Model 5. These results suggest that treatment of K as a fixed effect was unlikely to bias estimates in integrative models which were evaluated under the same assumptions as models 2 and 5.

Across all candidate growth models, the parameters estimated by Model 11 best predicted length at recapture across cross validation iterations and therefore represents the best estimated parameter set. Information from older/larger fish was very important for grounding the upper end of integrative growth curves resulting in parameters that better predicted length at recapture. Omission of the largest individuals from Models 1-5 resulted in lower estimates of L_{∞} , causing growth curves to asymptote prematurely. When Included, these additional data sources resulted in growth parameters that were better able to predict the length of fish recaptured from the MHI in the OTP study.

Additional data sources included here represent collections spanning several decades from the MHI and NWHI. When incorporating these additional data sources, it is an assumption that growth within the population did not differ significantly with time or region. With the exception of Ralston and Miyamoto (1983), all subsequent studies of growth for *P. filamentosus* in the Hawaiian archipelago have included data or parameter estimates from one or more previous studies in their calculations regardless of time and place of collection (DeMartini et al.

1994, Moffitt and Parrish 1996, Andrews et al. 2012). Genetic homogeneity between NWHI and MHI stocks provides some justification pooling data across both regions (Gaither et al. 2010, Gaither et al. 2011). However, these spatial and temporal assumptions may not reflect phenotypic realities and further work is required to resolve whether differences in growth exist between the two regions.

Sexual size dimorphism may explain the tendency of parameters obtained here and elsewhere to underestimate the length at recapture observed for the largest fish in the OTP dataset (approximate fork length > 50 cm) (Figure 4). If one sex attains a greater asymptotic length than the other, that sex is likely to be overrepresented in the largest size classes relative to the total population. In smaller sizes where the sex ratio of individuals is similar to the sex ratio of the total sampled population, averaging of model parameters between sexes results in increased estimates of variance. However, for the largest size classes where sex ratios are not representative of the population as a whole, estimated growth parameters continue to represent an average of both sexes and will result in underestimates of length at recapture for the larger, overrepresented sex while overestimating the length at recapture for the largest individuals of the other. While not pronounced, dimorphic size differences have been observed in a number of lutjanid species (Grimes, 1987; Mees, 1993; Newman et al., 2000; Newman and Dunk, 2002; Nichols, 2019; Taylor et al., 2018; Williams et al., 2017). Elsewhere in their distribution, larger asymptotic lengths have been reported for male *P. filamentosus* in the Seychelles while during research fishing in the Northwestern Hawaiian Islands, the number of females outnumbered males almost 2:1 in the largest size classes, and in Guam no differences between sexes were observed (Kami, 1973; Kikkawa, 1984; Mees, 1993). However, estimations of growth

parameters for *P. filamentosus* in the Central Pacific are sex agnostic and a method for non-invasive sexing of this species was unknown until recently (Luers et al. 2017).

Accurate estimates of von Bertalanffy growth parameters are very important for management. Growth parameters are often used directly or indirectly in stock assessment and fisheries management (Haight et al., 1993; Polovina et al., 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 from K using empirical relationships (Jensen, 1996; Ralston, 1987; Thorson et al., 2017). Underestimating K will underestimate M , characterizing a stock as less productive than it actually is while overestimating K will have the opposite effect. If a management regime is linked to such a flawed estimate of stock productivity, then the stock is likely to be mismanaged and under or over harvested, respectively, relative to its true biological potential. Future work to refine these estimates for *P. filamentosus* should consider that differences in life history may exist between males and females.

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Competing Interests

The authors declare that they have no competing interests.

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Tables

Table 1. Summary of tagging and recapture locations for *P. filamentosus* used for growth increment approaches as referenced to reporting grids in Figure 1. Adapted from Kobayashi, Okamoto & Oishi (2008).

Table 2. Estimates (and 95% confidence intervals when available) of von Bertalanffy growth parameters L_{∞} , K , and t_o reported by the present and prior studies.

Table 3. Von Bertalanffy growth parameter estimates from Bayesian hierarchical growth models (Models 1-4).

Table 4. A reference for the candidate model structures used to determine the preferred model structure from integrative maximum likelihood growth models (Models 5-11).

Table 5. Sample and Population Parameter Estimates (with bootstrapped confidence intervals) from Maximum Likelihood Growth Models (Models 5-11).

Figure Captions

Figure 1. Reporting Grid Map.

Map showing the location and number of the State of Hawaii's statistical reporting grids corresponding to the reported location of tagging and recaptured for fish summarized in Table 5.2.

Figure 2. Length and Time at Liberty for OTP Data.

*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 3. Coefficient of Variation for von Bertalanffy Growth Function Parameters.

*Coefficient of variation for 2 von Bertalanffy growth function parameters (Brody growth coefficient, K) and (Mean asymptotic length 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 4. Plots Comparing Predicted and Observed Length at Recapture.

Predicted lengths at recapture fit using parameter point estimates from Bayesian Models 1 and 2 and population parameter estimates from Maximum likelihood Models 5 and 11 compared to observed length at recapture. 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.

Table 1: Summary of OTP data

		RELEASE LOCATION																												Total				
		127	304	306	307	308	309	311	312	313	320	321	327	331	332	351	401	402	403	404	405	407	408	409	421	423	424	428	429	452	505	528		
TAGGING LOCATION	127							1																									1	
	304				1						2																						3	
	306			1							1																						2	
	307				5								1																				6	
	308			1		2						5																					8	
	309											2																					2	
	311							25	1						4																		30	
	312							1	1																								2	
	313				1				1						3																		5	
	320			1	3						24		1																					29
	321											31																					31	
	327				3						2		2																				7	
	331							46	2						128			4															180	
	332														1																		1	
	351														1																		1	
	401																	131															131	
	402																	1															1	
	403																	1															1	
	404																							1									1	
	405							1																	1								2	
	407														1																		13	
	408														1																		1	
	409																	4															5	
	421																	14						1									15	
	423											1						14						1									16	
424					1									4			3						3									11		
428							2	1						2																		5		
429							2					1		1			1															5		
452												1		1																		2		
505											1																					1		
528							2																									2		
No Recovery		1	3	44	278	35	2	582	168	5	333	429	84	875	1	1	937	7	1	1	2	2	293	4	20	16	9	8	5	2	1	2	4151	

Table 2: Growth estimates for P. filamentous in Hawaii

	Method	Region	Otolith Growth Bands					Linf (95% CI)	K (95% CI)	to (95% CI)	Source
			Otoliths	(Bomb-Carbon)	Pooled Otoliths	Monthly Length	Recaptured Fish				
Direct Aging	Daily Increments	NWHI	17	-	-	-	-	-	-	-	Moffitt (1980)
	Daily Increments	NWHI	N.R.	-	-	-	-	80.5	0.16	-	Ralston (1980)
	Daily Growth Integration	NWHI	64	-	-	-	-	78	0.146	-1.67	Ralston & Miyamoto (1983)*
	Daily Growth Integration	NWHI	64	-	-	-	-	66.4	0.235	-0.81	Ralston & Miyamoto (1983)
	Daily Increments & Integration	NWHI	N.R.	-	-	-	-	69.8	0.534	0.18	Radtke (1987)
	Daily Increments & Integration	MHI & NWHI	92	-	-	-	-	70.4 (63.9 - 76.9)	0.25 (0.20, 0.31)	-0.22 (-0.39, -0.06)	DeMartini et al. (1994)
	Annual Increments	NWHI	N.R.	-	-	-	-	97.1	0.31	0.02	Uchiyama & Tagami (1984)
	Daily Increments, Integration, & Radioisotopes	MHI & NWHI	100	33	3	-	-	67.5 (65.7, 69.3)	0.242 (0.185, 0.299)	-0.29 (-0.38, -0.20)	Andrews et. al (2012)
Growth Increment	Modal Progression	MHI	-	-	13			78	0.21	0	Moffit & Parrish (1996)*
	Mark Recapture	MHI	-	-	-	96		71.55	0.15	-	O'Malley (2015) - Gulland and Holt
	Mark Recapture	MHI	-	-	-	96		57.80 (55.97, 58.67)	0.28 (0.25, 0.31)	-	O'Malley (2015) - Francis
	Mark Recapture	MHI	-	-	-	387		65.92 (60.9 - 71.6)	0.24 (0.19 - 0.30)	-	Present Study - Francis
	Mark Recapture	MHI	-	-	-	387		59.7 (56.9 - 63.0)	0.32 (0.27 - 0.38)	-	Present Study - Bayesian Model 1
	Mark Recapture	MHI	-	-	-	387		60.2 (57.3 - 61.2)	0.35 (0.07 - 0.39)	-	Present Study - Bayesian Model 2
	Mark Recapture	MHI	-	-	-	387		76.8 (13.7 - 162.7)	0.17 (0.14 - 0.20)	-	Present Study - Bayesian Model 3
	Mark Recapture	MHI	-	-	-	387		77.3 (12.36 - 162.7)	0.24 (0.04 - 0.76)	-	Present Study - Bayesian Model 4
	Mark Recapture	MHI	-	-	-	387		61.0 (56.1, 66.7)	0.30 (0.23, 0.39)	-	Present Study - Maximum Likelihood Model 5
	Integrative	MHI & NWHI	113	33	3	13	378	67.6 (65.4, 69.6)	0.22 (0.12, 0.25)	-0.37 (-0.47, -0.28)	Present Study - Integrative Model 11

* Linf parameter constrained during fit

Table 3: Von Bertalanffy growth parameter estimates from Bayesia

	Parameter	Mean	SD	2.50%	Median	97.50%	R ²	n eff
Model 1	$L_{\infty\mu}$	59.89	1.58	57.10	59.80	63.24	1.00	2000
	$L_{\infty\sigma}$	5.47	0.34	4.80	5.46	6.15	1.00	36000
	$L_{\infty\tau}$	0.03	0.00	0.03	0.03	0.04	1.00	36000
	Shape	26.85	4.40	19.63	26.36	36.86	1.00	2500
	deviance	3351.95	120.29	3106.84	3355.69	3575.02	1.00	3700
	k_{μ}	0.32	0.03	0.27	0.32	0.37	1.00	1800
	k_{σ}	0.01	0.00	0.01	0.01	0.02	1.00	38000
	k_{τ}	10741.60	7970.11	2241.98	8492.59	32025.77	1.00	38000
	rate	10.52	1.59	7.88	10.35	14.10	1.00	2800
	τ	0.27	0.04	0.20	0.26	0.36	1.00	5700
	σ	3.85	0.60	2.77	3.82	5.11	1.00	5700
Model 2	$L_{\infty\mu}$	60.12	1.62	57.21	60.04	63.52	1.00	30000
	$L_{\infty\sigma}$	5.50	0.34	4.85	5.50	6.17	1.00	84000
	$L_{\infty\tau}$	0.03	0.00	0.03	0.03	0.04	1.00	84000
	Shape	26.64	4.21	19.63	26.24	36.04	1.00	7900
	deviance	3356.96	119.45	3110.59	3361.29	3578.22	1.00	28000
	k_{μ}	0.35	0.16	0.07	0.32	0.79	1.00	63000
	k_{σ}	1.14	85.41	0.01	0.10	3.24	1.00	84000
	k_{τ}	1294.41	3430.44	0.10	105.30	10874.77	1.00	84000
	rate	10.36	1.49	7.85	10.22	13.67	1.00	5200
	τ	0.26	0.04	0.19	0.26	0.36	1.00	21000
	σ	3.88	0.60	2.77	3.85	5.14	1.00	21000
Model 3	$L_{\infty\mu}$	76.89	31.95	17.19	74.42	160.86	1.00	84000
	$L_{\infty\sigma}$	88.68	4772.30	0.01	1.32	364.22	1.00	84000
	$L_{\infty\tau}$	570.00	2323.38	0.00	0.57	6238.55	1.00	84000
	Shape	62.32	13.32	41.03	60.49	92.62	1.00	1400
	deviance	3937.75	46.81	3847.12	3937.23	4030.55	1.00	41000
	k_{μ}	0.17	0.01	0.14	0.17	0.20	1.00	3200
	k_{σ}	0.02	0.00	0.01	0.02	0.03	1.00	8000
	k_{τ}	2543.07	807.09	1398.95	2400.92	4491.85	1.00	8000
	rate	17.93	3.84	11.85	17.41	26.63	1.00	1600
	τ	0.13	0.01	0.11	0.13	0.15	1.00	84000
	σ	7.92	0.61	6.80	7.89	9.20	1.00	84000
Model 4	$L_{\infty\mu}$	77.32	33.39	13.20	74.63	166.14	1.00	25000
	$L_{\infty\sigma}$	132.25	9204.30	0.01	1.65	429.54	1.00	84000
	$L_{\infty\tau}$	529.45	2244.18	0.00	0.37	5947.71	1.00	84000
	Shape	32.76	3.60	26.33	32.55	40.48	1.00	13000
	deviance	4090.50	39.61	4016.26	4089.51	4171.26	1.00	34000
	k_{μ}	0.24	0.18	0.04	0.18	0.77	1.00	84000
	k_{σ}	5.93	1357.98	0.01	0.09	3.67	1.00	84000
	k_{τ}	1293.51	3336.91	0.07	115.99	10767.12	1.00	84000

Table 4: Structure of integrative models (Models 5-11)

Data Source	Model 5	Model 6	Model 7	Model 8	Model 9	Model 10	Model 11
Growth Increment							
OTP	X	X	X	X	X	X	X
Mark Recapture							
Direct Aging							
Ralston & Miyamoto (1983)							
Integrated Daily Otolith Counts	-	X	X	X	X	-	-
Direct Aging							
Demartini et al. (1994)							
Otolith Microincrements	-	X	X	X	X	X	X
Direct Aging							
Andrews et al. (2012)							
Bomb Carbon	-	X	X	X	X	X	X
Direct Aging							
Andrews et al. (2012)							
Lead:Radium	-	X	X	X	X	X	X
Length Frequency							
Moffitt & Parrish (1996)							
Modal Progression	-	X	X	X	X	X	X
Weighting	NA	Equal	By n	Equal	By n	Equal	By n
Pooled Within Data Types?	NA	Yes	Yes	No	No	No	No

Table 5: Sample and Population Parameter Estimates

Parameter Estiamtes for Integrated Growth Models								
Parameter	Model 5		Model 6		Model 7			
	Sample	Population	Sample	Population	Sample	Population		
Linf_mu	60.92	60.98 (56.17,66.67)	77.96	66.79 (70.27, 78.69)	64.74	64.80 (61.91, 67.17)	66.87	
Linf_std	5.32	5.3 (4.53,6.07)	6.02	5.256 (4.00, 6.83)	5.62	5.57 (4.72, 6.36)	5.53	
K	0.300	0.299 (0.229,0.393)	0.122	0.189 (0.121, 0.235)	0.262	0.260 (0.231, 0.302)	0.253	
A_mu	0.95	0.95 (0.8,1.09)	1.5	1.21 (1.06, 1.50)	1	1.00 (0.92, 1.08)	0.99	
A_sig	0.19	0.19 (0.15,0.24)	0.13	0.16 (0.12, 0.19)	0.18	0.18 (0.14, 0.22)	0.18	
Sig	2.1	2.08 (1.50,2.55)	2.97	2.51 (2.05, 3.11)	2.2	2.20 (1.74, 2.62)	2.32	
t0	-	-	-0.86	-0.50 (-0.90, -0.34)	-0.31	-0.32 (-0.44, -0.20)	-0.27	
oto_sig	-	-	6.79	3.93 (1.31, 7.09)	1.82	1.76 (0.68, 3.03)	1.33	
lf_sig	-	-	1.33	3.06 (1.31, 4.06)	4.07	4.39 (3.86, 4.98)	3.93	

Parameter	Model 9		Model 10		Model 11			
	Sample	Population	Sample	Population	Sample	Population		
Linf_mu	64.74	64.80 (62.22, 67.03)	69.34	68.72 (65.23, 71.68)	68.52	67.55 (65.42,69.55)		
Linf_std	5.62	5.58 (4.74, 6.37)	4.26	4.08 (3.00, 5.11)	4.22	5.00 (4.26,5.68)		
K	0.261	0.26 (0.23, 0.30)	0.146	0.17 (0.13, 0.21)	0.173	0.219 (0.198,0.245)		
A_mu	1	1.00 (0.925, 1.08)	1.5	1.37 (1.19, 1.60)	1.34	1.11 (1.03,1.19)		
A_sig	0.18	0.18 (0.15, 0.22)	0.14	0.155 (0.119, 0.184)	0.16	0.17 (0.14,0.2)		
Sig	2.2	2.20 (1.75, 2.61)	3.29	2.99 (2.45, 3.62)	2.9	2.39 (2,2.77)		
t0	-0.31	-0.32 (-0.43, -0.21)	-0.8	-0.65 (-0.96, -0.43)	-0.63	-0.37 (-0.47,-0.28)		
oto_sig	1.82	1.74 (0.66, 2.94)	1.61	1.42 (0.97, 1.84)	1.4	0.96 (0.49,1.31)		
lf_sig	4.07	4.38 (3.88, 4.94)	1.43	2.41 (1.43, 3.29)	3.09	4.63 (4.15,5.15)		

Figure 1: Reporting Grid Map

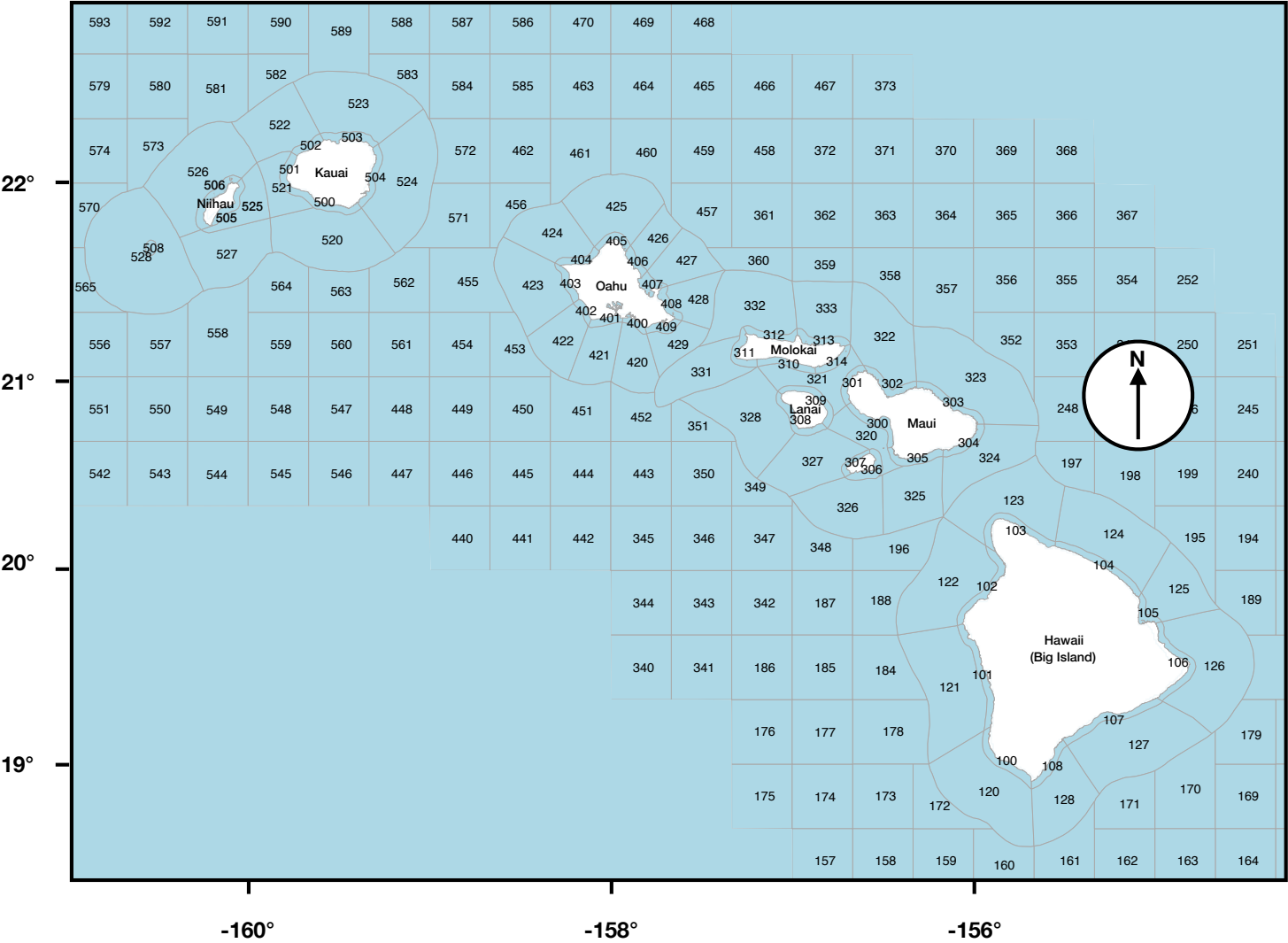


Figure 2: Length and Time at Liberty for OTP Data

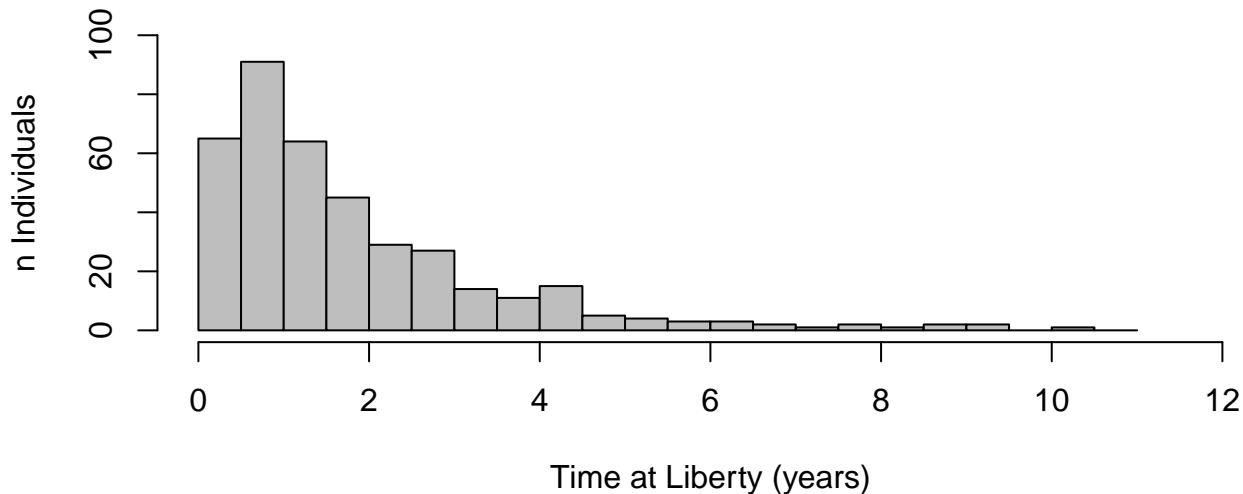
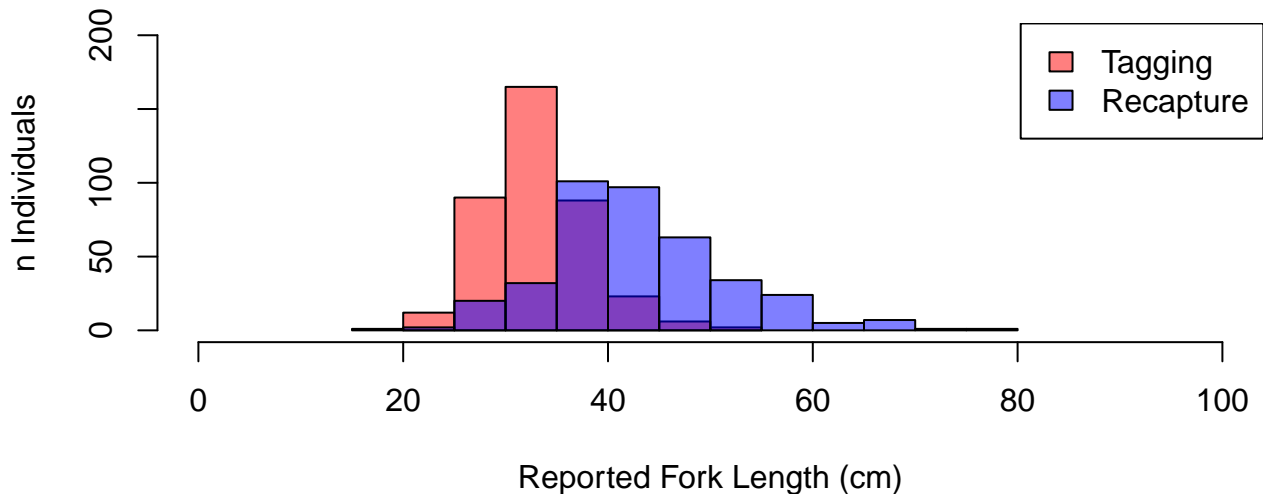


Figure 3: Coefficient of variation of growth function parameters

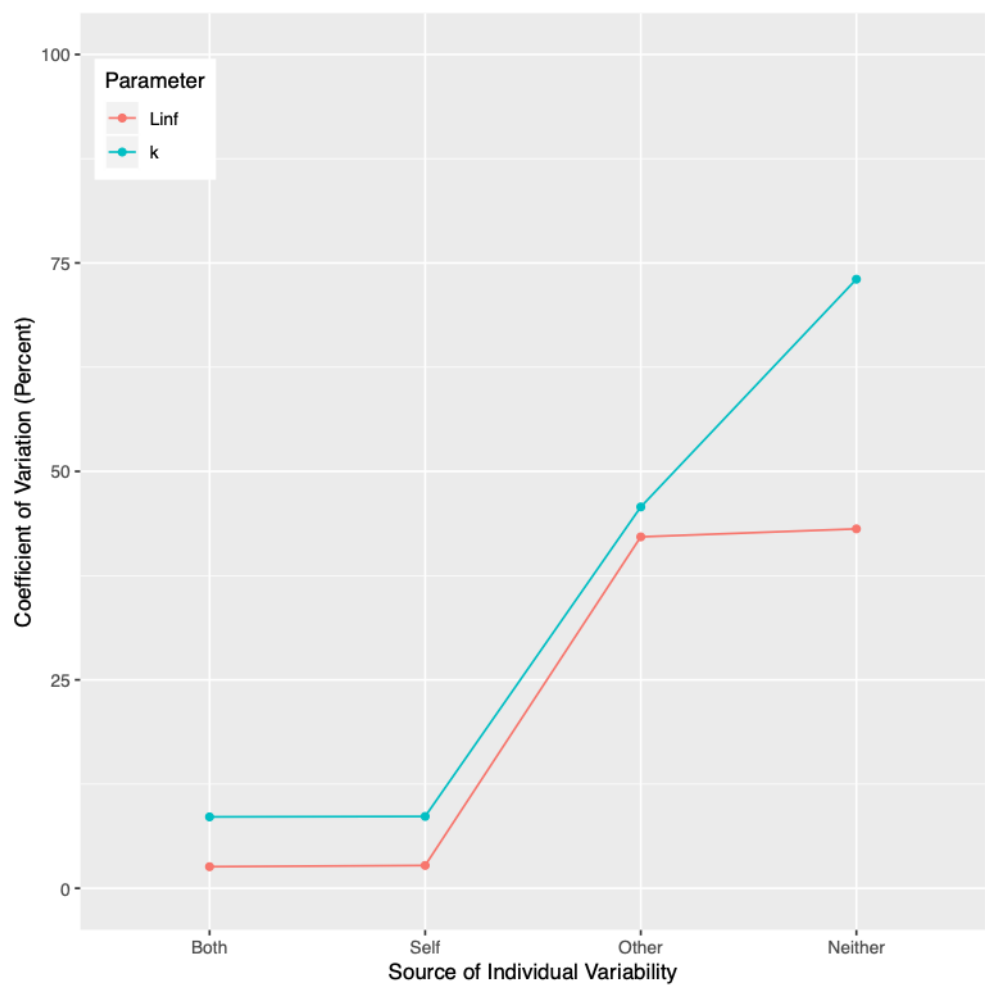
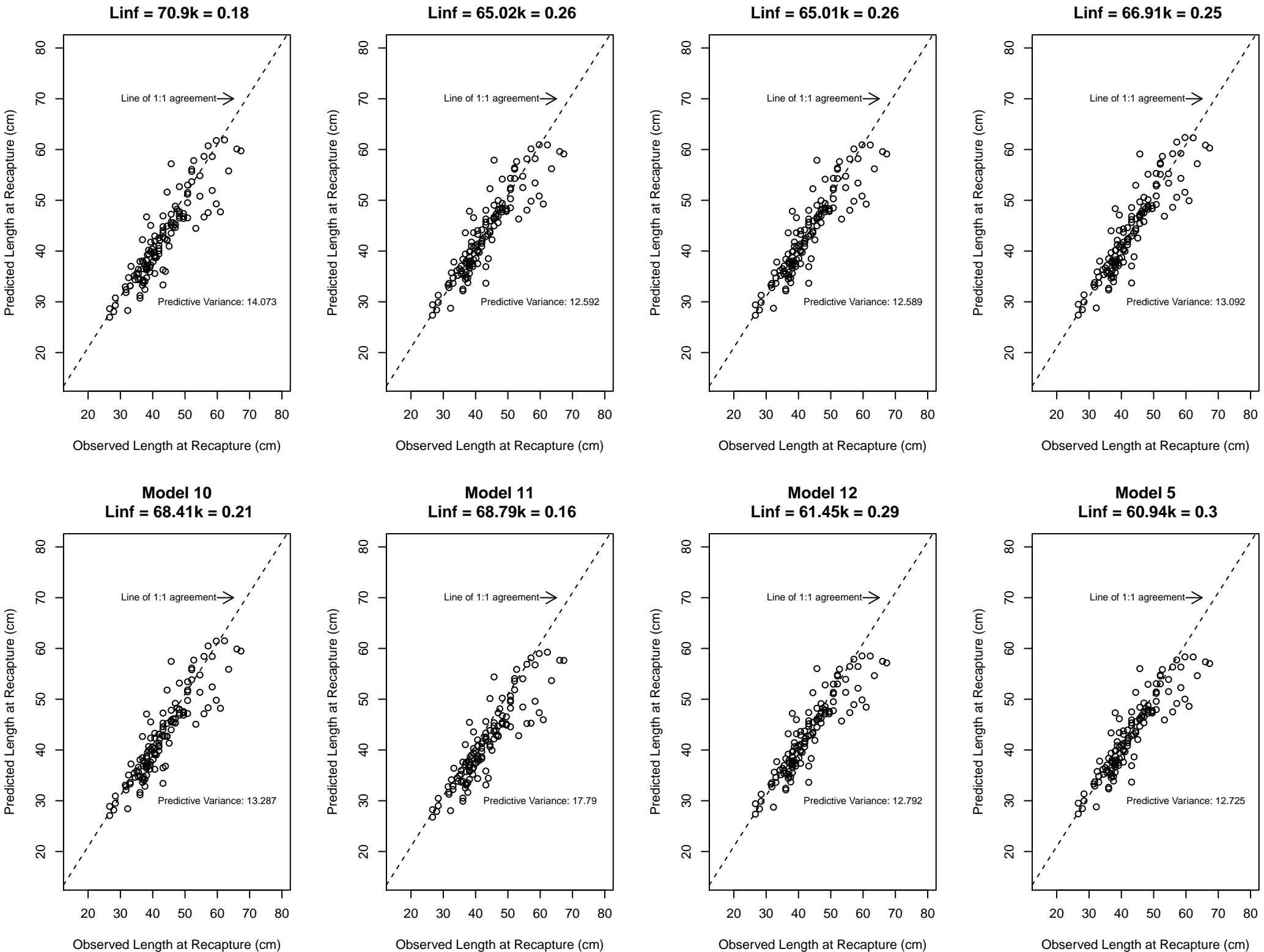


Figure 4: Plots comparing predicted and observed length at recapture



Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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