

Fisheries Research

Estimation of growth parameters integrating tag-recapture, length-frequency, and direct aging data using likelihood and Bayesian methods for the tropical deepwater snapper *Pristipomoides filamentous* in Hawaii

--Manuscript Draft--

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Abstract:	Pristipomoides filamentosus is an economically and culturally important species of deepwater snapper found throughout the Indo-Pacific. From 1989 to 1993, the State of Hawaii initiated a tagging program with scientists and fishers opportunistically recapturing fish to quantify regional growth and other life history parameters for the species. Over approximately 10 years, 10.5% of 4,179 tagged fish were recaptured. We used this data to compare von Bertalanffy growth parameters estimated using Bayesian and likelihood approaches. Next, we defined an objective cost function to estimate growth parameters that integrated the tagging data with direct aging and length frequency data used in previous regional growth studies. Our results reconcile 30+ years of effort from various methods to estimate growth parameters for <i>P. filamentosus</i> in Hawaii ($\bar{L} = 68.14$ cm FL 95% [95% Confidence Interval (CI): 65.42–69.54] and $K=0.22$ [CI: 0.20–0.25]), demonstrate the importance of individual variability in the species due primarily to the asymptotic length parameter, and suggest the effects of sexual dimorphism on growth as a focus of future inquiry. These results have direct management implications for the species as growth is a critical input for age-based stock assessment models and often used as a proxy for other life history traits.

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Dear Editors,

We would like to extend our thanks again to yourself and our reviewers for your time and effort in reviewing our manuscript. Your constructive feedback has vastly improved the clarity of our work. We express our thanks both here and in our acknowledgements section.

In the following document, we have presented the major comments of each reviewer and the changes that have been made to the manuscript to address them. Our responses are italicized. Additionally, a spreadsheet detailing the minor concerns of the reviewers is also included with our resubmission. This document outlines the line-specific comments of reviewers as well as how the comment has been addressed.

We hope the editor and reviewers find the improved manuscript satisfactory for publication.

Thank you again for your work, as it has improved our own,



Stephen R. Scherrer Ph.D.

On behalf of all authors.

Reviewer 1

Fishery Selectivity

The first concern is with respect to fishery selectivity. The tagging program was fishery-dependent and used hook-and-line gear, which likely selectively samples various size classes of fish; I didn't see this accounted for in your description of your likelihood function. An example of this penalty is pasted below from Kapur et al. (2019) – there is TMB code for estimation available online which accompanies this paper.

$$L(D|\theta) = \prod_i S_{L_i} \frac{1}{\sqrt{2\pi}\sigma a_i} e^{-(L_i - \hat{L}_i)/(2[\sigma a_i]^2)} / \int_{-\infty}^{\infty} S_l \frac{1}{\sqrt{2\pi}\sigma a_i} e^{-(\hat{L}_i - l)/(2[\sigma a_i]^2)} dl \quad (6)$$

where L_i is the observed length at a given age a_i , \hat{L}_i is the corresponding estimate based on VBGF parameters θ , S is a logistic selectivity function with parameter L_{50} , the length at which 50 % of individuals (male or

Kapur, M., Haltuch, M., Connors, B., Rogers, L., Berger, A., Koontz, E., Cope, J., Echave, K., Fenske, K., Hanselman, D., Punt, A.E., 2020. Oceanographic features delineate growth zonation in Northeast Pacific sablefish. Fish. Res. 222. <https://doi.org/10.1016/j.fishres.2019.105414>

Unfortunately, this dataset did not come with information on what gear was used to catch these fish, nor can we assume commercial fishers recapturing fish used standard gear. This makes accounting for gear selectivity non-trivial. We have instead implemented a sensitivity analysis per the suggestion of reviewer 3 that implicitly accounts for differences in catchability by synthesizing data such that the distribution of fish of all sizes is uniform. We can then compare the parameter estimates previously obtained to the estimates from fitting the same models to this synthetic data and determining how different the resulting parameters are. This provides an indication of the bias that sample size (which gear selectivity contributes to) imparts on the estimation process. The details of this analysis are found in Methods section 2.10 and Results Section 3.4 and summarized in table 6.

Lack of Priors

The second concern regards the implementation and presentation of the Bayesian model. Considering the previous work on growth for this species, it is strange that uninformative priors were used for all input parameters (line 120). Even a moderately broad prior (ie to account for sexual dimorphism) would be acceptable, but we do have a sense for the general range for this species. It is unsurprising that the MLE & Bayes methods performed similarly based on this setup, considering they used the same data source.

All four bayesian models have been refit using Linf and K parameters from Andrews et al. 2012 as priors.

It would simplify the reader's understanding of Model 1 vs Model 2 if you would use the language for hierarchical Bayesian models, whereby individual growth parameters are sampled

from a distribution. Please remove the line 125 where k is referred to as fixed, and simply state outright that k is estimated once for the entire population, same story for L129 regarding L infinity. This pops up several times (L171, “k is treated as fixed unknown parameter”) – just say it was estimated for the entire population.

We have updated the verbiage in the methods section to reflect reviewer 1's suggestions and ensured that consistency is maintained through the rest of the document.

Finally, it isn't clear to me if/how the MLE and Bayesian methods were compared aside from the bootstrapped intervals overlapping. You mention “cross validation iterations to determine model structure” L349, with no prior description of what this is or what it does – nor a definition of “mssr”. Once the corrections above are made, it would be useful to directly compare the best-fit model estimates from each approach.

MSSR (Mean sum of squared residuals) has been updated to a more conventional metric (RMSE - Root mean squared error). The best MLE model was determined through cross validation (see the methods section) but current computational constraints make cross validation with Bayesian models unfeasible. Instead we've used quantitative metrics to determine which Bayesian models are credible (CV, DIC), results of the sensitivity analysis, and similarity to MLE estimates.

Reviewer 3

Sensitivity Analysis

When comparing model 11 with models 1-5, the authors show that the inclusion of additional growth data improved the predictive capacity of growth models compared to tagging data alone (Lines 356 - 359), likely due to the "omission of the largest individuals from models 1-5" (line 410). Along those lines, my main suggestion for the authors is to conduct a sensitivity analysis for the influence of the distribution of samples in their data (i.e. varied representation of samples by age class).

Since this approach assumes individual variability, it is important to have sampled the entire distribution of length at age for results to be accurate. The authors' integrated approach addresses this, but not completely. Assuming that sampling was sufficient to describe the true mean and standard deviation of length at age, simulating observations from a distribution such that each age class is equally represented and then re-fitting the growth model could provide a metric to compare the results of the model fit to the raw data with for detecting this influence. Samples in the oldest age classes are unlikely to represent the full distribution of lengths at age, as large and old fish are naturally scarce. This, and general underrepresentation of older age classes compared to younger ones can bias the estimation of L_∞ in some cases. This was suggested by the authors as a possible reason for differences in their results when compared to those of O'Malley et al. (2015) (line 380) and in discussing differences between model 11 and models 1-5 (lines 408 - 411). Indeed, this has also been suggested in publications providing recommendations for age and growth studies and describing their fundamentals (e.g. Cailliet and Tanaka 1990), but is not frequently examined quantitatively (e.g. Bolser et al. 2018). It is possible that model 11 included enough data such that this effect is negligible, but we do not know for sure unless a sensitivity analysis is conducted. Examining differences between models fit to the raw data and models fit

to a dataset with equal representation of samples at age would allow the authors to identify if the distribution of samples has influenced their results.

Differences in sample distribution can also confound comparisons between studies and sexes, such as the ones made in the discussion of the present study (paragraphs beginning on lines 381 & 425). In my opinion, it would be worth reviewing the sample distribution of the datasets associated with the studies being compared, if they are available, to identify differences in sample distribution that could confound comparisons (e.g. a disparity in samples at older ages).

The authors did an excellent job of acknowledging the influence of sample distribution - particularly where estimation of L_∞ is concerned - in the portions of text mentioned thus far, but an explicit analysis would greatly enhance this paper and strengthen their conclusions.

A sensitivity analysis has been implemented using Bolser et al. 2018 as a framework. Methods and results of this analysis can be found under sections 2.10 and 3.4 respectively and summarized in table 6.

Line	Reviewer	Comment	Addressed	Notes
57	R3	Typo in Mark	x	Minor edits have been made throughout
117	R3	Zhang et al	x	It's unclear what the reviewer means by
334	R3	Line 334: 'e\x	x	Recommended Change Made
346	R3	this underes	x	Addressed using the sensitivity analysis.
	R3	if not becau	x	Added the following sentence: "These dif
	R3	I recommen	x	Figure 2 has been modified to show the
125	R1	Please remove	x	We've maintained the "fixed" terminolo
349	R1	Finally, it isn't	x	The best MLE model was determined thr
Title	R1	The title and a	x	We've removed age from the title
33	R1	is this the same	x	This dataset was considered for some of
31	R1	I found many s	x	Minor edits have been made throughout
68	R1	I found many s	x	Minor edits have been made throughout
57	R1	Other minor ty	x	Minor edits have been made throughout
Equation 1	R1	Equation 1 you	x	Only the last recapture was included. The
	137 R1	L137 "...presu	x	Recommended Change Made
Abstract	R1	At least in the	x	Included as 95% CI
	R1	Some of the la	x	Phrasing "Integrative" and "Integrated" v
MLE Section	R1	Please label th	x	Referenced in table 4
	349 R1	L349 define "M	x	MSSR has be replaced with RMSE (Root r
	147 R1	Similar to proc	x	Edited this line to read "Samples thinned
Figure 2	R1	make these col	x	The colors have been changed so that th

: for clarity while retaining sentence content. This particular example is among them
this. It is possible they are confusing the standard normal distribution with the normal distributi

Note that the integrative models do include large fish, which improved esimation, however the
difference may represent genetic or phenotypic differences between these populations, or difference:
distributions of the additional length-at-age and growth increment data
try to maintain consistancy with Zhang et al. (2009) but have more clearly defined it earlier in the
through cross validation (see the methods section) but current computational constraints make cr

the candidate integrative models, but was omitted under the preffered integrative model
: for clarity while retaining sentence content. This particular example is among them
: for clarity while retaining sentence content. This particular example is among them
: for clarity while retaining sentence content. This particular example is among them
e parameter t has been renamed delta_t and the j subscript removed for clarity.

was used to reflect the same terminology of Eveson et al., to make this clear, all use of the phras

mean squared error)

I at an interval of 1/50 (number kept = 28,000) to reduce potential autocorrelation between seq
e overlapping region is more distinct.

ion, the latter being synonymous with the gaussian distribution

model structure that best predicted recapture length used a modest weighting with these additions in the methods and sampling distribution between studies."

the manuscript using the reviewer's suggested terminology.

oss validation with Bayesian models unfeasible. Instead we've used quantitative metrics to determine

se integrated now refers to mathematical integration while integrative is used to refer specifically to sequential values or strings of values in the posterior distributions. "

tional samples. Model 10 was identical to Model 11 except it applied a greater weight to this ad

ermine which Bayesian models are credible (CV, DIC), results of the sensitivity analysis, and simil

γ to the methods and outputs of models including additional data sources

ditional data and resulted in less precise estimates of recapture length. Parameters from both of

arity to MLE estimates.

f these models have the same residual pattern, so under-inclusion of large individuals does not i

explain this observation.

1 *Estimation of growth parameters integrating tag-recapture, length-frequency, and direct aging*
2 *data using likelihood and Bayesian methods for the tropical deepwater snapper*
3 *Pristipomoides filamentosus in Hawaii*

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43

44 ***Abstract***

45 *Pristipomoides filamentosus* is an economically and culturally important species of deepwater
46 snapper found throughout the Indo-Pacific. From 1989 to 1993, the State of Hawaii initiated a
47 tagging program with scientists and fishers opportunistically recapturing fish to quantify regional
48 growth and other life history parameters for the species. Over approximately 10 years, 10.5% of
49 4,179 tagged fish were recaptured. We used this data to compare von Bertalanffy growth
50 parameters estimated using Bayesian and likelihood approaches. Next, we defined an objective
51 cost function to estimate growth parameters that integrated the tagging data with direct aging and
52 length frequency data used in previous regional growth studies. Our results reconcile 30+ years
53 of effort from various methods to estimate growth parameters for *P. filametosus* in Hawaii
54 ($L_{\infty}=68.14$ cm FL 95% [95% Confidence Interval (CI): 65.42–69.54] and K=0.22 [CI: 0.20–
55 0.25]), demonstrate the importance of individual variability in the species due primarily to the
56 asymptotic length parameter L_{∞} , and suggest the effects of sexual dimorphism on growth as a
57 focus of future inquiry. These results have direct management implications for the species as
58 growth is a critical input for age-based stock assessment models and often used as a proxy for
59 other life history traits.

60

61 ***1. Introduction***

62 *Pristipomoides filamentosus* (Valenciennes, 1830) is a species of long-lived deepwater snapper
63 distributed throughout the tropical Indo-Pacific (Allen, 1985; Gaither et al., 2011). The species
64 constitutes a significant fraction of Hawaii's commercial bottomfish fishery where it is
65 colloquially known as opakapaka (Ralston and Polovina 1982, Langseth et al. 2018). Opakapaka
66 is one of seven management unit species pooled for stock assessment of Hawaii's bottomfish,

67 however there is interest in the potential use of species-specific, age-structured assessments for
68 this fishery which require accurate life history estimates of growth and other life history
69 parameters (Langseth et al., 2018; Mauder et al., 2015, Oyafuso et al. 2017).

70 A number of studies have used different approaches to estimate growth parameters for *P.*
71 *filamentosus* in Hawaii and elsewhere in the Indo-Pacific (Table 2). Early estimates were
72 obtained using direct aging approaches with length-at-age data from otolith reads interpreted as a
73 proxy for age (Ralston & Miyamoto, 1983; Uchiyama & Tagami, 1984; Radtke, 1987;
74 DeMartini, Landgraf & Ralston, 1994, Ralston & Williams, 1988). These methods relied on the
75 integration of daily otolith bands which can bias age estimates due to episodic growth and poor
76 increment resolution in early (< 5 years) life stages (Wakefield et al., 2017). Revised parameter
77 estimates using the direct aging approach were obtained by supplementing datasets from those
78 previous studies with additional length-at-age data where ages were estimated using bomb
79 radiocarbon and lead-radium ratios (Andrews et al., 2012). In addition, a length frequency
80 approach was used to estimate growth parameters by tracking the modal length progression of
81 juvenile cohorts caught in nursery habitat in Kaneohe Bay, Hawaii. However, this study used a
82 previous estimate of L_{∞} where individual variability was not considered; this omission can result
83 in biased parameter estimates (Sainsbury, 1980, Moffitt and Parrish, 1996). Estimation of growth
84 estimates from an ongoing mark-recapture study (separate from the results reported here) has
85 attempted using growth increment approaches but preliminary results have been limited by the
86 size distribution of recaptured individuals and the use of a parameterization of von Bertalanffy's
87 growth function (VBGF) that is not compatible with direct aging and length frequency
88 approaches (R. I. C. C. Francis, 1988; O'Malley, 2015). While the methods of each
89 aforementioned studies produced individual estimates of growth parameters, none of the studies

90 attempted to integrate all three classes of data (i.e., direct aging, modal progression, growth
91 increment from tagging) to explicitly evaluate the parameter values and sources of uncertainty.

92 Analytical and statistical advances for estimating growth have developed to account for
93 sources of variability and permit parameter comparisons across length-at-age, length frequency,
94 and tagging based approaches (Eveson et al., 2004; R. I.C.C. Francis, 1988; Wang et al., 1995).

95 Structural modifications to Fabens (1965) parameterization of the VBGF address issues of
96 compatibility between growth parameters from direct aging and length frequency approaches
97 with those derived from tagging studies (Maller and Deboer 1988, James 1991, Palmer et al.

98 1991, Laslett et al. 2002, Eveson et al. 2004, 2007, Zhang et al. 2009). These methods use
99 maximum likelihood and Bayesian frameworks to accommodate individual variability by
100 describing population parameters using probability distributions (R. I.C.C. Francis, 1988;

101 Kimura et al., 1993; Wang et al., 1995; Zhang et al., 2009). Bayesian approaches allow K and
102 L_∞ to be sampled in this manner and can account for prior information when estimating

103 parameters (Zhang et al. 2009). Maximum likelihood approaches typically estimate K once for
104 the entire population (henceforth referred to as “fixed”) but flexibility in their implementation
105 has allowed for the development of model structures that can estimate a single set of growth
106 parameters from direct aging, length frequency, and growth increment data simultaneously
107 (Wang et al. 1995, Laslett et al. 2002, Eveson et al. 2004).

108 Here, we derive growth parameters using Bayesian and maximum likelihood methods
109 applied to a previously unreported dataset from a cooperative tagging program for *P.*
110 *filamentosus* in the Main Hawaiian Islands (MHI) with fishers opportunistically recapturing fish
111 and reporting to the State of Hawaii’s Division of Aquatic Resources. Parameters estimated from
112 these data using a Bayesian framework are compared to a maximum likelihood approach

113 integrating tagging data with length-at-age and length frequency data previously used to describe
114 growth in *P. filamentosus* in the Main Hawaiian Islands (MHI) and Northwestern Hawaiian
115 Islands (NWHI). These new growth estimates are compared to those previously reported for *P.*
116 *filamentosus* the Hawaiian Archipelago.

117

118 **2. Materials and Methods**

119 *2.1 Opakapaka Tagging Program*

120 Tagging data used for this analysis were obtained by biologists from Hawaii's Division of
121 Aquatic Resources (DAR) within the state's Department of Land and Natural Resources
122 (DLNR). Between 1989 and 1993 the Opakapaka Tagging Program (OTP), led by staff biologist
123 Henry Okamoto operated from fishing vessels contracted out of Honolulu Harbor, tagging and
124 releasing 4,179 *P. filamentosus* in total. All tagging occurred in the MHI with coarse location
125 data for the site of tagging and recapture recorded using the commercial statistical reporting grid
126 (Table 1, Figure 1). Tagging effort concentrated primarily around the island of Oahu and the
127 Maui Nui complex which includes the islands of Maui, Molokai, Lanai and Kahoolawe. Since
128 1990, these areas have accounted for approximately 67.7% of Hawaii's commercial bottomfish
129 harvest. Fewer than 1% of fish in this study were tagged offshore of the islands of Niihau and
130 Hawaii (Big Island).

131 Fish were caught with hook-and-line gear and brought to the surface at a rate of 2-5 feet
132 per second. Prior to tagging, each fish was placed in a holding container with aerated seawater to
133 assess their likelihood of surviving. Fish appearing lively and upright were deemed suitable
134 candidates for tagging. If the stomach was inverted and full of gas, it was punctured using a
135 small sharp instrument (e.g., scalpel, hypodermic needle, fishhook). A few scales were carefully

136 removed and a small surgical incision (~1 cm) was made near the fish's anal opening to assist in
137 expelling gas from the body cavity. A uniquely identifiable monofilament streamer tag was
138 anchored within and protruded from this incision. The fork length of each fish was recorded to
139 the nearest ¼ inch in addition to the location and time of capture before returning the fish to the
140 sea headfirst with downward momentum attempting to counteract buoyancy due to any
141 residual gas.

142 Local commercial and recreational fishers were made aware of the program through fliers
143 distributed at the local fish markets, to fish dealers, at fishing supply outlets, and posted at small
144 boat harbors and recaptured fish were reported up to a decade after they were tagged (Kobayashi
145 et al., 2008; Okamoto, 1993). Fishers were incentivized with a \$10 reward to report the date,
146 location, and depth that each fish was landed and the fish's fork length. When recaptured by OTP
147 personnel, tagged fish were fitted with an additional tag and released again.

148

149 *2.2 Tagging Data Management*

150 The data collected by OTP was entered into a spreadsheet and subsequent analysis was
151 performed using R (R Core Team, 2014), the Bayesian statistical software JAGS (Plummer,
152 2003), and the R package R2Jags (Su and Yajima, 2012). The dataset was filtered to remove
153 records of individuals that were never recaptured, individuals for which the tagging date,
154 recapture date, or tag ID was not recorded, and individuals that were not the species of interest.
155 Fork lengths for the remaining fish recorded at tagging and recapture were linearly transformed
156 from inches to centimeters prior to model fitting for consistency with growth parameters
157 estimated elsewhere. Incremental growth (Δl) and time at liberty (Δt) were calculated for each
158 fish. When individuals were recaptured on more than one occasion, Δl and Δt were only

159 calculated between the first marking event and the final recapture so as to not violate model
160 assumptions of independence. Fish with Δt less than 60 days were excluded from the dataset.

161

162 *2.3 Parameter Estimation from Tagging Data: Bayesian Approach*

163 Growth parameters were estimated for the *P. filamentosus* tagging data following the Bayesian
164 methodology of Zhang et al. (2009). This approach uses a Fabens version of the VBGF but
165 allows the parameters to vary among individuals. Hence the predicted length of a captured
166 individual is expressed as:

167
$$(E1) \quad L_i = L_{\infty,i} (1 - e^{-K_i(A_i + \Delta t_i)})$$

168 This is parameterized such that $L_{i,j}$ is the length of individual i when the individual is captured
169 (that is, when an individual is initially captured and marked and again during the final recapture
170 event), Δt_i is the time-at-liberty (time between initial capture and the last recapture) for the i th
171 individual when it was recaptured. This term is zero when the equation is used to calculate the
172 individual's length at capture. A_i is the relative age of i th individual at tagging (age minus Δt_i).

173 Parameters K and L_∞ are the VBGF parameters for the i th individual drawn from Gaussian
174 distributions defining the population means. Prior growth parameter estimates reported by
175 Andrews et al. (2012) were used to inform model priors for K and L_∞ parameters. Uninformative
176 priors were used for all other input parameters, using Gaussian, gamma, beta, and uniform
177 distributions following the approach of Zhang et al. (2009).

178 The hierarchical Bayesian model which allowed both the K and L_∞ parameters to vary
179 across individuals, by sampling these parameters from the distribution of hyperparameters, as
180 described above is henceforth referred to as Model 1. This model was compared to three
181 additional models fit with various constraints to K and L_∞ . Model 2 estimated the K parameter

182 once for the entire population (henceforth referred to as “fixed”) while accounting for variation
183 across individuals by sampling L_∞ from hyperparameter distributions. Model 3 treated L_∞ as a
184 fixed parameter while sampling K parameter from hyperparameter distributions, and both
185 parameters were fixed under Model 4.

186 Evaluating the restrictive assumptions of models 2-4 was accomplished by comparing
187 growth parameters to those estimated by Model 1. Model 1 is the presumptive best estimate for
188 *P. filamentosus* VBGF parameters, since it allows the most flexible incorporation of individual
189 variability by sampling both L_∞ and K from hyperparameters. If a given parameter is relatively
190 stable when the parameter varies across individuals and when it was treated as fixed for the
191 population, then it might be inferred that treating this parameter on an individual basis is not
192 warranted. However, if parameter estimates differed when the parameter was fixed, then it might
193 be inferred that treating this parameter on an individual basis is necessary. Model 4 would *a*
194 *priori* be most similar to the Fabens approach, with both fixed K and L_∞ , but with the added
195 feature of estimating ages at initial tagging, A_i . It is the inclusion of this term that models growth
196 as a function of age, rather than length, allowing for direct comparison between parameters
197 estimated using tagging data and those obtained from direct-age and length frequency
198 approaches (Wang et al., 1995).

199 For each Bayesian model, the first 150,000 samples from the posterior distribution were
200 treated as burn-in and discarded from the Monte Carlo simulation. Additional samples were
201 thinned at an interval of 1/50 (number kept = 30,000) to reduce potential autocorrelation between
202 sequential values or strings of values in the posterior distributions. Initial starting estimates of K
203 and L_∞ were obtained from Andrews et al. (2012) with two additional chains run simultaneously
204 with initial starting values 50% lower and 100% higher. This resulted in nearly identical

205 solutions as shown in Table 3. The mean K and L_∞ values from the posterior distribution were
206 used as metrics of population values. Median values deviated from mean values by less than one
207 half of 1 percent (Table 3), indicative of symmetrical distributions easily characterized by any
208 descriptor of value tendency (i.e., mean, median, or mode). Convergence was also ascertained by
209 examination of the Gelman-Rubin statistic (Gelman and Rubin, 1992).

210 The fit of each model was assessed by calculating a Bayesian p-value from the posterior
211 predictive distribution. Bayesian p-values were simulated using the model's posterior
212 distribution and test whether simulated data is more extreme than the observed data. Bayesian P-
213 values range between 0 and 1 where values approaching 0.5 indicate the model is a good fit to
214 the data, while extreme values near 0 or 1 indicate that the model does not adequately represent
215 the data (Meng, 1994). The deviance information criterion (DIC) was used to compare between
216 models.

217

218 *2.4 Parameter Estimation from Tagging Data: Maximum Likelihood Approach*

219 The maximum likelihood approach of Laslett et al. (2002) was used to fit Model 5 using the
220 following equation,

221
$$(E2) \quad l_{ij} = \mu_\infty(1 - e^{-K(a_i + \Delta t_i)}) + \varepsilon_{ij}$$

222 This method derives growth parameters from the joint distribution of an individual's length at
223 tagging and recapture. This is most similar in approach to Model 2 of the Bayesian approach in
224 that asymptotic length, L_∞ , is treated as a normal random effect $N(\mu_\infty, \sigma_\infty^2)$, accounting for
225 differences between an individual the total population, while K is treated as a fixed unknown
226 parameter. Rather than using length increments to fit observed growth, a bivariate normal joint
227 distribution of lengths recorded at marking and recapture is used to estimate each individual's

228 age at tagging (a_i). The distribution of a_i across all individuals (A) is treated as a random effect
229 with a lognormal distribution $L(\mu_{logA}, \sigma_{logA}^2)$. Measurement error is also treated as a random
230 normal distribution $N(0, \sigma^2)$. An unconditional joint density is then derived for each individual
231 by integrating their individual joint distribution with respect to a . This process is described in
232 greater detail by Laslett et al. (2002).

233 This approach was used to estimate values of the growth parameters μ_∞ , σ_∞^2 , K , μ_{logA} ,
234 σ_{logA}^2 , and σ^2 by minimizing of the negative log-likelihood cost function obtained from summing
235 the unconditional joint density $h(l_1, l_2)$ of each individual (E3).

236

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

237 Two-sided 95% confidence intervals (2.5%, Median, 97.5%) were estimated for each parameter
238 through a bootstrapping procedure repeated for 10,000 iterations. During each bootstrap
239 iteration, the model was refit using data randomly resampled with replacement from the original
240 tagging data.

241

242 *2.5 Estimation of Integrated Growth Parameters using sources of growth data*

243 Datasets previously used by other studies to quantify the growth of *P. filamentosus* in the MHI
244 and NWHI were combined with OTP tagging data to produce a single set of integrated parameter
245 estimates using a modified form of the method proposed by Eveson, Laslett, and Polacheck
246 (2004). Additional datasets that were included represent both direct aging and length frequency
247 approaches and are briefly described below. In total, 6 candidate models (Models 6-11) were fit
248 using this approach (Table 4).

249

250 2.6 Parameter Estimation: Length Frequency Data
251 Length frequency data consisted of the size distributions of juvenile *P. filamentosus* sampled
252 over 13 months between October 1989 and February 1991 as reported by Moffitt and Parrish
253 (1996). The reported fork lengths of captured fish were binned in 1 cm increments and presented
254 in 13 histograms corresponding to each month of sampling. The data was reconstructed by
255 overlaying a series of evenly spaced horizontal lines across the Y-axis of each histogram
256 corresponding to the addition of a single fish. The reconstructed data contained 1,048
257 observations, one more than was reported by the original study (Moffitt and Parrish, 1996).

258 The reconstructed length frequency data were incorporated into integrated models by
259 following the two-step method described in Laslett et al. 2004. In the first step, a Gaussian
260 mixture model was fit using maximum likelihood and used to decompose the distribution of fork
261 lengths for each recruitment cohort present for each month of data. This was done using the
262 normalmixEM function from the mixtools package in R (Benaglia et al., 2009) by assuming the
263 mean of each distribution corresponded to the observed mode. A bimodal Gaussian mixture
264 model was fit for the data collected between the months of October-February, as the original
265 study reported that two cohorts were present during this period. A single cohort was present the
266 remainder of the year. In the second step, estimated mean fork length, $\hat{\mu}_{ijk}$, and standard error,
267 s_{ijk} , of each cohort during each month of sampling was used to estimate growth parameters
268 using the following parameterization of the VBGF (E4).

$$269 \quad (E4) \quad \hat{\mu}_{ijk} = \mu_{\infty} \left(1 - e^{-K(a_{ijk} - a_0)} \right) + e_{ijk} + \varepsilon_{ijk}$$

270 With this parameterization, i , j , and k reflect the fishing year, month, and age cohort,
271 respectively. The estimated age of each cohort at each sampling period is denoted by a_{ijk} . Ages
272 were estimated relative to the month of July when peak spawning of *P. filamentosus* occurs,

resulting in age estimates between 3 and 19 months (Luers et al., 2017).. Sampling and residual model errors were described using random normal distributions. 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 mean 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.

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

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

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

283

284 2.7 Parameter Estimation: Direct Aging Data

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

292 The details of the method used to estimate growth parameters from direct aging data are
293 described in detail in Eveson et al. 2004. Briefly summarized, parameters are modeled using the
294 VBGF parametrization described by equation E9.

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

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

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

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

300 Where l_i denotes the length of the i^{th} fish, at age a_i and a_0 is a fixed parameter analogous to t_0
 301 when a fish has a hypothetical length of zero. As with the model for tagging data, $l_{\infty i}$ is the
 302 individual asymptotic length of the i^{th} fish drawn from the random normal distribution $L_{\infty} =$
 303 $N(\mu_{\infty}, \sigma_{\infty})$. γ_i represents the distribution of individual measurement error and is similarly
 304 random, drawn from the distribution $\gamma = N(0, \sigma_{\gamma})$. The log-likelihood cost function derived
 305 from these equations is described by the following equation (E12).

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

307
308 2.8 Defining an objective cost function and estimating integrated growth parameters
309 To derive integrated growth parameters across tag-recapture, direct aging, length frequency, and
310 growth increment data sources, we developed an appropriate integrated cost function, defined
311 from the sum of the cost functions for each data source and a set of scaling constants, β_i (E13).
312 The single set of growth parameters best describing all data sources is obtained through
313 minimization of the integrated cost function, Λ (E13).

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

315 The six candidate model structures (Models 6-11) for estimating growth in P .
316 *filamentosus* were developed and evaluated by permutating the value of scaling constants, the

317 pooling of datasets using similar approaches, and whether length-at-age data where age estimates
318 were obtained through integration of daily otolith bands were included (Table 4). Two
319 approaches were used for the value of scaling constants (β_i). The first weighted scaling constants
320 for every data source so that each source contributed equally to the resulting parameter estimates
321 while the second weighted each source proportionate to its number of observations. Other
322 differences between integrated models included whether the four direct aging data sources
323 contributed individually to the integrated cost function or if they were first pooled. Omitting
324 direct aging data where ages were estimated by integrating daily growth increments was also
325 considered as this method is likely to underestimate age (Table 4; Wakefield et al 2017).

326

327 *2.9 Model Evaluation*

328 The six candidate integrated models (Models 6-11) were evaluated using a repeated cross
329 validation procedure to determine the model structure that best predicted the growth observed in
330 the OTP data (Burman, 1989). During each iteration of this procedure, two thirds of fish in the
331 OTP dataset ($n = 258$) were randomly selected without replacement for model training while the
332 remaining third ($n = 129$) were used to test model performance. Performance was assessed by the
333 ability of each parameter set, fit using the training data, to predict the expected length at
334 recapture for fish in the test data by calculating the root mean squared error (RMSE) between the
335 predicted and observed growth. The preferred model was the one who's structure most
336 frequently resulted in the lowest RMSE over 10,000 iterations. To determine if incorporating
337 additional data sources improved predictive performance, RMSE for the preferred integrated
338 model was then compared to the structure of Model 5 which included only tagging data.

339 Once the structure of the preferred integrated model was determined, two-sided 95%
340 confidence intervals were estimated for each parameter from 10,000 bootstrap iterations. As with
341 tagging data, the procedure for resampling direct aging data was straightforward and involved
342 random sampling with replacement to construct synthetic datasets with an equal number of
343 observations as the original data. Bootstrapping length frequency data was done by hierarchical
344 sampling such that the study periods in each bootstrapped dataset were resampled from the
345 corresponding periods of the original data.

346

347 *2.10 Sensitivity Analysis*

348 The accuracy of growth parameters can be affected by the distribution of individuals sampled
349 relative to that of the total population (Bolser et al., 2018, Calliet and Tanaka 1990). Gear
350 selectivity, sampling location, variation in annual recruitment, and other factors can lead to under
351 representation of select size and age classes in the sample population (Goodyear 2019, Kapur et
352 al., 2020).

353 A sensitivity analysis was performed to quantify the effect of the sampled distribution on
354 parameter estimates with an approach inspired by the approach of Bolser et al. (2018). This was
355 done by first segmenting the OTP data in 5-cm increment bins by the length of each individual
356 recorded during tagging. Then a synthetic dataset was constructed for each model by simulating
357 additional individuals using the mean of each bin and the standard deviation within that bin
358 calculated from the tagging data, until all bins contained the same number of observations (200).
359 Growth in synthetic data was estimated using parameters obtained for each model and the mean
360 time at liberty for all fish in the OTP study. Each model was then refit using its corresponding
361 synthetic dataset. The influence of sampling distribution on parameters L_∞ and K was quantified

362 as the amount synthetic estimates differed from estimates from observed data. This type of
363 approach does not explicitly account for differences in selectivity or differences between the
364 sampled and true population structure, but it can fill critical gaps caused by these issues by
365 flattening the number of observations across size classes (Bolser 2018).

366

367 **3. Results**

368 *3.1 Opakapaka Tagging Program*

369 In total, 487 recaptures were recorded for 439 unique individuals for a recapture rate of
370 10.5% (Table 1). Mortality of fish upon release appeared to be generally low, likely due to the
371 selection of healthy fish in good condition. Some immediate mortality was observed due to
372 capture stress and predation by sharks and cetaceans (4 individuals). Long-term mortality was
373 thought to be relatively low based upon the high rates of tag return spanning many years. Hydra
374 (small cnidarian polyps) biofouling of the tags was observed for some individuals with large
375 times at liberty, with some lesions apparent around the opening where the tag exited the body
376 cavity. This was not thought to be a serious health issue since the fish appeared to be feeding and
377 swimming normally.

378 Initial fork length at capture across all individuals ranged in size from 16.5 to 53.3 cm
379 (mean = 31.9 cm, standard deviation (s.d.) = 5.5) and ranged from 19.1 cm and 52.8 cm (mean =
380 32.8, s.d. = 5.1) for fish that were later recaptured. For those fish that were later recaptured, fork
381 length measured at recapture was between 22.9 cm and 76.2 cm (mean = 41.9, s.d. = 8.7). The
382 minimum time at liberty for any fish between tagging and recapture was a single day while the
383 maximum time at liberty was 10.3 years (3,748 days) (Figure 2). The mean time at liberty was
384 1.82 years or 666 days (s.d. = 625).

385 One fish was excluded from further analysis as its initial fork length at capture was not
386 recorded so growth could not be calculated. Seven fish were removed because the recapture date
387 was not properly recorded and therefore their time at liberty could not be determined. Of the
388 remaining 432 fish recaptured, 351 were recaptured a single time, 33 fish were recaptured a total
389 of two times, one fish recaptured 3 times, and two fish were recaptured 4 times. We also
390 excluded from analysis 45 individuals for whom time at liberty was less than 60 days to
391 minimize the influence of any short-term tagging effects. This process yielded a data set
392 consisting of 387 unique individuals.

393

394 *3.2 Estimating Growth Parameters from Tagging Data: Bayesian Approach*

395 The Bayesian hierarchical approach produced mean estimates of L_{∞} and K for Models 1–4
396 (Table 3). Model 1, which incorporated individual variability in both L_{∞} and K , yielded mean
397 parameter estimates of $L_{\infty} = 61.4$ cm (coefficient of variation [c.v.] = 2.56) and $K = 0.30$ (c.v. =
398 8.33). L_{∞} and K parameter estimates for Model 2, where K was fixed, were 61.61 cm (c.v. =
399 2.72) and 0.29 (c.v. = 45.6) respectively. Under Model 3, where L_{∞} was fixed and K was fit
400 freely $L_{\infty} = 72.0$ cm (c.v. = 41.0) and $K = 0.19$ (c.v. = 8.67) and $L_{\infty} = 74.82$ cm (c.v. = 42.71)
401 and $K = 0.17$ (c.v. = 72.91) for Model 4, where both parameters were fixed. Additional
402 parameters for each of the four models are presented in Table 3. The Gelman-Rubin convergence
403 criteria indicated that the model solutions were credible, with asymptotic convergence clearly
404 occurring after ~4000 iterations, well within the burn-in phase of the Bayesian modeling runs.
405 All 4 models appeared to fit the the data well; the mean Bayesian P-values from all retained
406 posterior samples for all models ranged between 0.500 and 0.501. Model 4 had the lowest DIC
407 (4780.7) followed by Model 3 (5216.3), and Model 2 (8644.5), while Model 1 had the highest

408 DIC (8826.8), however treating model parameters as fixed under models 2-4 resulted in large
409 coefficients of variation suggesting that accounting for individual variability is important, with
410 perhaps variability in L_∞ being more important based upon the low coefficient of variation in L_∞
411 from the base case of Model 1 and the large coefficients seen in Model 3 and Model 4 (Figure 3).

412

413 *3.3 Parameter estimation using maximum likelihood*

414 The maximum likelihood approach used for Model 5 converged to produce estimates of μ_∞ , σ_∞^2 ,
415 K , $\mu_{\log A}$, $\sigma_{\log A}^2$, and σ^2 (Table 5). Bootstrap confidence intervals of parameters μ_∞ and K
416 overlapped L_∞ and K parameters from Bayesian models 1 and 2 (Table 2). From these results, it
417 was concluded that estimates produced by maximum likelihood approaches were satisfactorily
418 similar to estimates from the Bayesian approach. Model residuals appeared homoskedastic and
419 normally distributed around zero for all but the largest fish. For fish with recapture lengths
420 exceeding 60 cm, growth models underestimated observed recapture lengths (Figure 4).

421

422 *3.4 Comparing model performance*

423 Across all 10,000 cross validation iterations to determine the preffered integrated model
424 structure, the six candidate models produced RMSE values that ranged between 2.78 and 4.95
425 (mean = 3.9, s.d. = 0.3) with lower values indicating a better fit to the data. The structure of
426 Model 11 outperformed competing models during cross validation (2,192 of 10,000 iterations).
427 RMSE for this model ranged between 2.9 and 4.9 (mean = 3.9, s.d. = 0.3).

428 The inclusion of additional growth data improved the predictive capability of growth
429 models compared to tagging data alone. The structure of Model 11 performed better than the
430 structure of Model 5 during cross validation (5,672 of 10,000 iterations). Differences in RMSE

431 between the competing structures of Model 11 and Model 5 ranged between -1.2 and 0.1 (mean
432 = -0.1, s.d. = 0.1) with structure of Model 5, fit exclusively using tagging data, producing RMSE
433 values that ranged between 2.8 and 5.3 (mean = 3.9, s.d. = 0.3). Bootstrapped parameter
434 estimates refit using the structure of the preferred integrated model (Model 11) and the tagging
435 only structure of Model 5 are summarized in Table 2 and all parameters for models 5-11 are
436 reported in full in Table 5.

437

438 *3.5 Sensitivity Analysis*

439 Parameters estimated using the observed and synthetic data differed by as much as 95.74% but
440 was generally less than 3.30%. For all models, the K parameter differed more between the
441 synthetic and observed data than the parameter L_∞ . Estimates of L_∞ and K from the preferred
442 integrated model (Model 11) estimated from synthetic data differed from the observed data by
443 0.69% and 2.46% respectively. These differences between the observed and synthetic data were
444 smaller than those for all other maximum likelihood models and second smallest overall.
445 Parameter estimates for Model 1, the Bayesian model that accounted for individual differences in
446 each parameter and had the lowest coefficient of variation across both parameters, differed by
447 1.23% for the L_∞ parameter and 4.09% for K . Parameters for Model 4, the Bayesian model with
448 the lowest DIC score, differed between observed and synthetic data by 0.22% in the L_∞
449 parameter and by 1.04% in K , the lowest of any model. Sensitivity results for all models are
450 reported in full for all models in table 6.

451

452 **4. Discussion**

453 Our integrated model results reconcile 30+ years of effort to quantify growth for *P. filamentosus*
454 in the Hawaiian Archipelago and provides robust support for some previously estimated
455 parameter values. Growth parameters derived using integrated models incorporating additional
456 length frequency and length-at-age data were better able to predict the growth observed in
457 recaptured fish compared to those fit using only tagging data. These parameters were in
458 agreement with direct aging studies where ages were estimated using 1) the fit of only integrated
459 daily growth increments from otoliths collected in the NWHI without constraining L_{∞} (Ralston
460 and Miyamoto, 1983), 2) integrated daily growth increments and microincrement counts
461 (DeMartini et al. 1994), and 3) the radioisotopic composition of otolith material and counts of
462 otolith increments from the MHI and NWHI (Andrews et al. 2012) and support the implicit
463 assumption that tagging individuals did not significantly disrupt their growth trajectory.
464 integrated parameters differed from estimates from an ongoing mark recapture study in the MHI
465 which reported faster growth and smaller asymptotic lengths (O'Malley, 2015). These
466 differences could arise from real changes in growth rate between the periods fish were collected,
467 methodological differences in model interpretation, and/or that thus far, none of the fish
468 recaptured during the ongoing study have been of the largest size classes (maximum size
469 reported = 47.6 cm FL).

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

476 differences may represent genetic or phenotypic differences between these populations, or
477 differences in the methods and sampling distribution between studies.

478 Of the Bayesian models, Model 1 was presumed optimal because it incorporated
479 individual variability in both L_∞ and K parameters, however this model performed the worst of
480 all Bayesian models during sensitivity testing. Models 2-4 suggest that individual variability in
481 both K and L_∞ parameters is important, with perhaps variability in L_∞ being more important
482 based on the similar parameter estimates obtained from Models 1 and 2 and comparison of
483 relatively small the coefficient of variation for L_∞ from the base case of Model 1 to the larger
484 coefficients of variation under assumptions of constrained individual variability in Model 3 and
485 Model 4 (Figure 3). Based upon these parameter estimates and pattern of large standard
486 deviations, it is likely Models 3 and 4 were not credible despite lower DIC values and
487 performing well during sensitivity testing. Similar parameter estimates obtained from Models 1
488 and 2 suggested that the primary source of individual variability was due to variability in the L_∞
489 parameter. This is consistent with other studies where the best models accounted for individual
490 variability in both terms but accounting for individual variation in the L_∞ term alone was
491 sufficient to describe growth while significantly reducing computational complexity (Eveson et
492 al. 2007, Zhang et al. 2009).

493 The treatment of individual variability in parameters for Model 2 were identical to those
494 used to fit Model 5 (OTP data only). Comparing growth parameter estimates from these models
495 indicate that Bayesian and maximum likelihood fitting methods performed similarly. Parameter
496 estimates for Models 1 and 2 were contained within the 95% confidence intervals of Model 5.
497 These results suggest that treatment of K as a fixed effect was unlikely to bias estimates in

498 integrated models, fit using maximum likelihood, which were evaluated under the same
499 assumptions as models 2 and 5.

500 Of all models presented, Model 11 appears to be the most predictive and robust. Across
501 all candidate integrated growth models, the parameters estimated by Model 11 were best
502 predictive of length at recapture during cross validation. This model was also the second most
503 robust to the sensitivity analysis, with parameter estimates differing by less than 2.5%. While
504 information from older/larger fish from direct aging datasets was very important for grounding
505 the upper end of integrated growth curves and resulted in parameters that better predicted length
506 at recapture, these additional data sources were less influential to this model than for the model
507 otherwise identical in structure (Model 10) that placed a greater emphasis on these data sources.
508 This suggests that the inclusion of additional data was important for obtaining accurate results
509 but were most helpful when their influence was limited.

510 Additional data sources included here represent collections spanning several decades
511 from the MHI and NWHI. When incorporating these additional data sources, it is an inherent
512 assumption that growth within the population did not differ significantly with time or region.
513 This is not the first study to make these assumptions; with the exception of Ralston and
514 Miyamoto (1983), all subsequent studies of growth for *P. filamentosus* in the Hawaiian
515 archipelago have included datasets or parameter estimates from one or more previous studies in
516 their calculations without regard to the time and place the data was collected (DeMartini et al.
517 1994, Moffitt and Parrish 1996, Andrews et al. 2012). Genetic homogeneity between NWHI and
518 MHI stocks provides some justification pooling data across both regions, however these spatial
519 and temporal assumptions may not reflect phenotypic realities and further work is required to

520 resolve whether differences in growth exist between the two regions (Gaither et al. 2010, Gaither
521 et al. 2011).

522 Sexual size dimorphism may explain the tendency of parameters obtained here and
523 elsewhere to underestimate the length at recapture observed for the largest fish in the OTP
524 dataset (approximate fork length > 50 cm) (Figure 4). For sex agnostic models, parameters are
525 essentially averaged between sexes. In smaller sizes classes where the sex ratio of individuals is
526 similar to that of the total population, this averaging of parameters between sexes results in
527 increased estimates of variance. However, if dimorphic differences in growth are present and one
528 sex disproportionately attains a greater asymptotic length than the other, that sex is likely to be
529 overrepresented in the largest size classes relative to the total population. Growth estimated for
530 these individuals continues to represent an average of both sexes and will result in the
531 underestimation of lengths at recapture, while growth in the underrepresented sex will be
532 overestimated. This produces a residual pattern resembling the one seen in the OTP data.

533 While not pronounced, dimorphic size differences have been observed in a number of
534 lutjanid species (Grimes, 1987; Mees, 1993; Newman et al., 2000; Newman and Dunk, 2002;
535 Nichols, 2019; Taylor et al., 2018; Williams et al., 2017). Elsewhere in their distribution, larger
536 asymptotic lengths have been reported for male *P. filamentosus* in the Seychelles while during
537 research fishing in the Northwestern Hawaiian Islands, the number of females outnumbered
538 males almost 2:1 in the largest size classes, and in Guam no differences between sexes were
539 observed (Kami, 1973; Kikkawa, 1984; Mees, 1993). These differences may be true sexual
540 dimorphism or discrepancies between the structure of the sampled and true populations.
541 Estimation of growth parameters for *P. filamentosus* in the Central Pacific have thus far
542 remained sex agnostic and a method for non-invasive sexing of this species was unknown until

543 recently (Luers et al. 2017). More work addressing sex specific differences is required to
544 adequately test for dimorphism in this region.

545 Accurate estimates of von Bertalanffy growth parameters are very important for
546 management. Growth parameters are often used directly or indirectly in stock assessment and
547 fisheries management (Haight et al., 1993; Polovina et al., 1987). These efforts are sensitive to
548 both growth parameters and the model used to estimate those parameters. For example, the rate
549 of instantaneous natural mortality M is a value of interest often inferred from K using empirical
550 relationships (Jensen, 1996; Ralston, 1987; Thorson et al., 2017). Underestimating K will
551 underestimate M , characterizing a stock as less productive than it actually is while
552 overestimating K will have the opposite effect. If a management regime is linked to such a
553 flawed estimate of stock productivity, then the stock is likely to be mismanaged and under or
554 over harvested, respectively, relative to its true biological potential. Future work to refine these
555 estimates for *P. filamentosus* should consider the role that dimorphic differences that may exist
556 between males and females may have on their respective life histories.

557

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569

570 ***Competing Interests***

571 The authors declare that they have no competing interests.

572

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- 748
- 749

750 **Tables**

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

754

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

757

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

760

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

763

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

766

767 **Table 6.** Parameter estimates obtained from a sensitivity analysis where tagging data was
768 divided into 5 cm bins and then synthetic data was added so that each bin contained 200
769 observations. Comparing parameter estimates fit to synthetic data against those from the original
770 dataset provide a metric to compare the effect of the sampling distribution on the estimates
771 obtained.

772 **Figure Captions**

773 **Figure 1. Reporting Grid Map.**

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

777

778 **Figure 2. Length and Time at Liberty for OTP and Additional Data.**

779 *The length of *P. filamentosus* recaptured and included in analysis of OTP tagging data and
780 the distribution of times at liberty are presented in subplots a and b respectively. The fork
781 length of fish during tagging is highlighted in blue while length at recapture is shown in red.
782 Subplot c shows the measured fork length and estimated ages from the various sources of
783 length at age data included in models 6 – 10 while subplot d tracks the mode fork length for
784 cohorts included in the length frequency data originally presented by Moffitt and Parrish
785 (1996), also used to supplement OTP data in models 6-10.*

786

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

788 *Coefficient of variation for 2 von Bertalanffy growth function parameters (Brody growth
789 coefficient, K and mean asymptotic length, L_∞) for *P. filamentosus*. Individual variability was
790 examined incorporating individual variability in both parameters, in either one of the
791 parameters in series, or in neither parameter.*

792

793 **Figure 4. Plots Comparing Predicted and Observed Length at Recapture.**

794 *Predicted lengths at recapture compared to the observed lengths at recapture for tagged P.*
795 *filamentosus. Length at recapture was predicted as a function of length at marking, time at*
796 *liberty, and parameter point estimates. The 1:1 line indicates where points would fall if model*
797 *parameters perfectly predicted length at recapture.*

Table 1

	RELEASE LOC															
	127	304	306	307	308	309	311	312	313	320	321	327	331	332	351	401
TAGGING LOCATION																
127							1									
304					1						2					
306			1								1					
307				5									1			
308			1		2						5					
309						2						2				
311							25	1						4		
312							1	1								
313					1			1					3			
320			1	3						24		1				
321					3						31					
327									2			2				
331							46	2					128			4
332													1			
351													1			
401															131	
402																1
403																1
404																
405								1								
407													1			
408													1			
409																4
421																14
423											1					14
424					1								4			3
428								2	1				2			
429								2			1		1			1
452											1		1			
505											1					
528								2								
No Recovery	1	3	44	278	35	2	582	168	5	333	429	84	875	1	1	937
Total	1	3	47	291	38	2	662	174	5	363	470	88	1022	1	1	1110

ATION

	402	403	404	405	407	408	409	421	423	424	428	429	452	505	528	Total
																1
																3
																2
																6
																8
																2
																30
																2
																5
																29
																31
																7
																180
																1
																1
																131
																1
																1
																1
																2
																13
																1
																5
																15
																16
																11
																5
																5
																2
																1
																2
	7	1	1	2	2	293	4	20	16	9	8	5	2	1	2	4151
	7	1	1	2	2	312	4	21	16	9	8	5	2	1	2	4671

Table 2

				Otolith Growth Bands	Otoliths (Bomb-Carbon)	Pooled Otoliths (Lead-Radium)	Monthly Length Frequency	Recaptured Fish	Linf (95% CI)	K (95% CI)	to (95% CI)	Source
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 57.80	-	0.15 0.28	-	-	O'Malley (2015) - Gulland and Holt
	Mark Recapture	MHI	-	-	-	96	(55.97, 58.67)	(0.25, 0.31)	-	-	-	O'Malley (2015) - Francis
	Mark Recapture	MHI	-	-	-	387	61.35 (58.16 - 65.03)	(0.24 - 0.35)	-	-	-	Present Study - Bayesian Model 1
	Mark Recapture	MHI	-	-	-	387	74.24 (39.9 - 140.69)	(0.03 - 0.22)	-	-	-	Present Study - Bayesian Model 4
	Mark Recapture	MHI	-	-	-	387	62.95 (56.17, 66.67)	(0.23, 0.39)	-	-	-	Present Study - Maximum Likelihood Model 5
	Integrative	MHI & NWHI	113	33	3	13	378 68.14 (65.42, 69.54)	(0.20, 0.25)	0.22 (-0.47, -0.28)	-0.37	-	Present Study - Integrative Model 11

* Linf parameter constrained during fit

Table 3

	Parameter	Mean	SD	2.50%	Median
Model 1	Linf_mu	61.35	1.77	58.16	61.26
	Linf_std	5.29	0.35	4.61	5.29
	Linf_tau	0.04	0.00	0.03	0.04
	Shape	31.22	5.34	22.44	30.64
	deviance	3403.95	104.18	3187.05	3408.58
	k_mu	0.30	0.03	0.24	0.29
	k_std	0.01	0.00	0.00	0.01
	k_tau	16638.56	11206.64	3514.55	13801.69
	rate	11.75	1.84	8.72	11.55
Model 2	tau	0.21	0.03	0.16	0.21
	variance	4.81	0.68	3.55	4.78
	Linf_mu	61.63	1.84	58.35	61.52
	Linf_std	5.33	0.35	4.66	5.32
	Linf_tau	0.04	0.00	0.03	0.04
	Shape	30.85	5.02	22.50	30.33
	deviance	3407.26	102.70	3192.68	3411.91
	k_mu	0.29	0.04	0.22	0.29
	k_std	0.02	0.02	0.01	0.01
Model 3	k_tau	9920.78	9897.17	226.69	6882.50
	rate	11.52	1.71	8.65	11.35
	tau	0.21	0.03	0.16	0.21
	variance	4.83	0.68	3.57	4.80
	Linf_mu	74.44	31.01	0.96	74.92
	Linf_std	249.92	45369.72	0.01	1.33
	Linf_tau	569.32	2373.11	0.00	0.56
	Shape	62.36	13.73	40.77	60.37
	deviance	3849.87	47.19	3759.04	3849.34
Model 4	k_mu	0.17	0.02	0.14	0.17
	k_std	0.02	0.00	0.01	0.02
	k_tau	2940.66	1053.97	1529.56	2740.53
	rate	17.71	3.91	11.61	17.12
	tau	0.12	0.01	0.10	0.12
	variance	8.49	0.68	7.26	8.46
	Linf_mu	74.24	30.90	0.49	74.68
	Linf_std	77.14	2436.28	0.01	1.30
	Linf_tau	576.32	2356.43	0.00	0.59
	Shape	33.43	3.78	26.65	33.19
	deviance	3988.08	39.95	3912.48	3987.16
	k_mu	0.16	0.03	0.10	0.16
	k_std	0.02	0.02	0.01	0.01

k_tau	9901.19	9929.88	236.54	6813.09
rate	9.38	0.99	7.60	9.32
tau	0.10	0.01	0.09	0.10
variance	10.15	0.74	8.80	10.11

97.50%	Rhat	n_eff
65.03	1.00	2000.00
5.99	1.00	36000.00
0.05	1.00	36000.00
43.43	1.00	2500.00
3594.17	1.00	3700.00
0.35	1.00	1800.00
0.02	1.00	38000.00
45752.82	1.00	38000.00
15.94	1.00	2800.00
0.28	1.00	5700.00
6.21	1.00	5700.00
65.60	1.00	30000.00
6.03	1.00	84000.00
0.05	1.00	84000.00
42.17	1.00	7900.00
3596.17	1.00	28000.00
0.36	1.00	63000.00
0.07	1.00	84000.00
36624.34	1.00	84000.00
15.38	1.00	5200.00
0.28	1.00	21000.00
6.22	1.00	21000.00
141.12	1.00	84000.00
369.43	1.00	84000.00
6155.82	1.00	84000.00
93.66	1.00	1400.00
3944.71	1.00	41000.00
0.20	1.00	3200.00
0.03	1.00	8000.00
5532.10	1.00	8000.00
26.64	1.00	1600.00
0.14	1.00	84000.00
9.91	1.00	84000.00
140.69	1.00	25000.00
351.70	1.00	84000.00
6321.73	1.00	84000.00
41.50	1.00	13000.00
4068.81	1.00	34000.00
0.22	1.00	84000.00
0.07	1.00	84000.00

36702.03	1.00	84000.00
11.50	1.00	21000.00
0.11	1.00	45000.00
11.69	1.00	45000.00

Table 4

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

Model 11
X
-
X
X
X
X
By n
No

Table 5

Parameter	Parameter Estimates for Int			
	Model 5		Model 6	
	Sample	Population	Sample	Population
Linf_mu	62.95	60.98 (56.17, 66.67)	77.96	66.79 (70.27, 78.69)
Linf_std	5.07	5.3 (4.53, 6.07)	6.02	5.256 (4.00, 6.83)
K	0.275	0.299 (0.229, 0.393)	0.122	0.189 (0.121, 0.235)
A_mu	0.98	0.95 (0.8, 1.09)	1.5	1.21 (1.06, 1.50)
A_sig	0.17	0.19 (0.15, 0.24)	0.13	0.16 (0.12, 0.19)
Sig	2.5	2.08 (1.50, 2.55)	2.97	2.51 (2.05, 3.11)
t0	-	-	-0.86	-0.50 (-0.90, -0.34)
oto_sig	-	-	6.79	3.93 (1.31, 7.09)
If_sig	-	-	1.33	3.06 (1.31, 4.06)

Parameter	Model 9		Model 10	
	Sample	Population	Sample	Population
Linf_mu	64.74	64.80 (62.22, 67.03)	69.34	68.72 (65.23, 71.68)
Linf_std	5.62	5.58 (4.74, 6.37)	4.26	4.08 (3.00, 5.11)
K	0.261	0.26 (0.23, 0.30)	0.146	0.17 (0.13, 0.21)
A_mu	1	1.00 (0.925, 1.08)	1.5	1.37 (1.19, 1.60)
A_sig	0.18	0.18 (0.15, 0.22)	0.14	0.155 (0.119, 0.184)
Sig	2.2	2.20 (1.75, 2.61)	3.29	2.99 (2.45, 3.62)
t0	-0.31	-0.32 (-0.43, -0.21)	-0.8	-0.65 (-0.96, -0.43)
oto_sig	1.82	1.74 (0.66, 2.94)	1.61	1.42 (0.97, 1.84)
If_sig	4.07	4.38 (3.88, 4.94)	1.43	2.41 (1.43, 3.29)

egrated Growth Models

Model 7		Model 8	
Sample	Population	Sample	Population
64.74	64.80 (61.91, 67.17)	66.87	66.89 (63.90, 70.10)
5.62	5.57 (4.72, 6.36)	5.53	5.31 (2.61, 6.25)
0.262	0.260 (0.231, 0.302)	0.253	0.25 (0.21, 0.29)
1	1.00 (0.92, 1.08)	0.99	0.98 (0.89, 1.10)
0.18	0.18 (0.14, 0.22)	0.18	0.18 (0.15, 0.21)
2.2	2.20 (1.74, 2.62)	2.32	2.36 (1.94, 2.93)
-0.31	-0.32 (-0.44, -0.20)	-0.27	-0.27 (-0.43, -0.17)
1.82	1.76 (0.68, 3.03)	1.33	1.30 (0.47, 3.14)
4.07	4.39 (3.86, 4.98)	3.93	4.32 (3.53, 5.03)

Model 11	
Sample	Population
68.14	67.55 (65.42, 69.55)
4.90	5.00 (4.26, 5.68)
0.214	0.219 (0.198, 0.245)
1.124	1.11 (1.03, 1.19)
0.16	0.17 (0.14, 0.2)
2.66	2.39 (2, 2.77)
-0.37	-0.37 (-0.47, -0.28)
1.04	0.96 (0.49, 1.31)
3	4.63 (4.15, 5.15)

Table 6

Model	Linf - Sensitivity	Linf - Original Fit	% Difference in Linf	K - Sensitivity
<i>Model 5</i>	62.24	62.95	-1.13	0.29
<i>Model 6</i>	76.73	77.96	-1.58	0.13
<i>Model 7</i>	65.59	64.74	1.31	0.27
<i>Model 8</i>	62.24	66.89	-6.95	0.29
<i>Model 9</i>	62.24	64.74	-3.86	0.29
<i>Model 10</i>	62.24	69.34	-10.24	0.29
<i>Model 11</i>	67.67	68.14	-0.69	0.22
<i>Bayesian Model 1</i>	62.1	61.35	1.23	0.31
<i>Bayesian Model 2</i>	72.1	61.63	16.98	0.18
<i>Bayesian Model 3</i>	73.8	74.44	-0.86	0.17
<i>Bayesian Model 4</i>	74.07	74.24	-0.22	0.17

K - Original Fit % Difference in K

0.27	3.94
0.12	2.62
0.26	4.43
0.25	12.9
0.26	9.44
0.15	95.65
0.21	2.46
0.3	4.09
0.29	-36.3
0.17	4.83
0.16	1.04

Figure 1

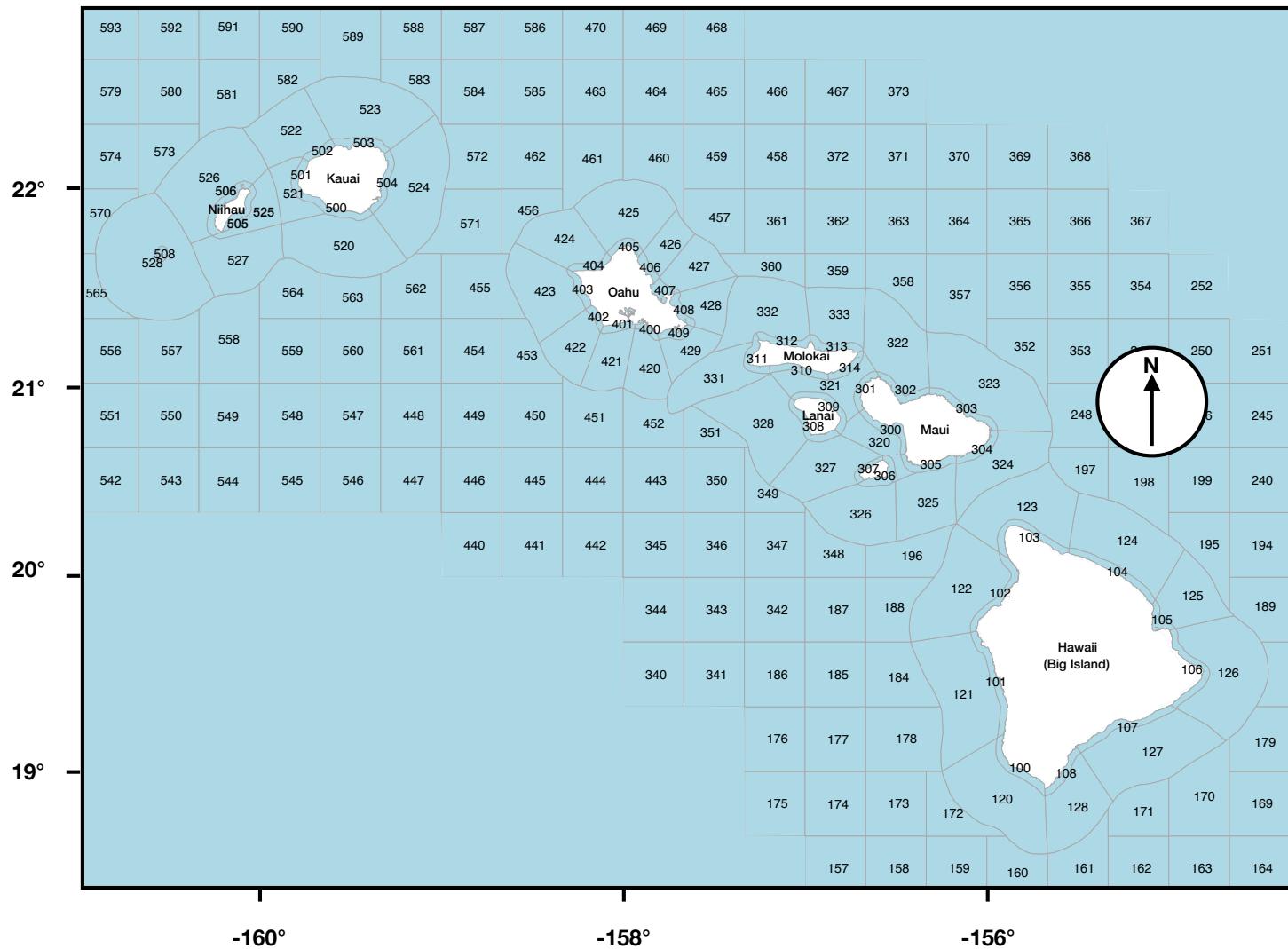


Figure 2

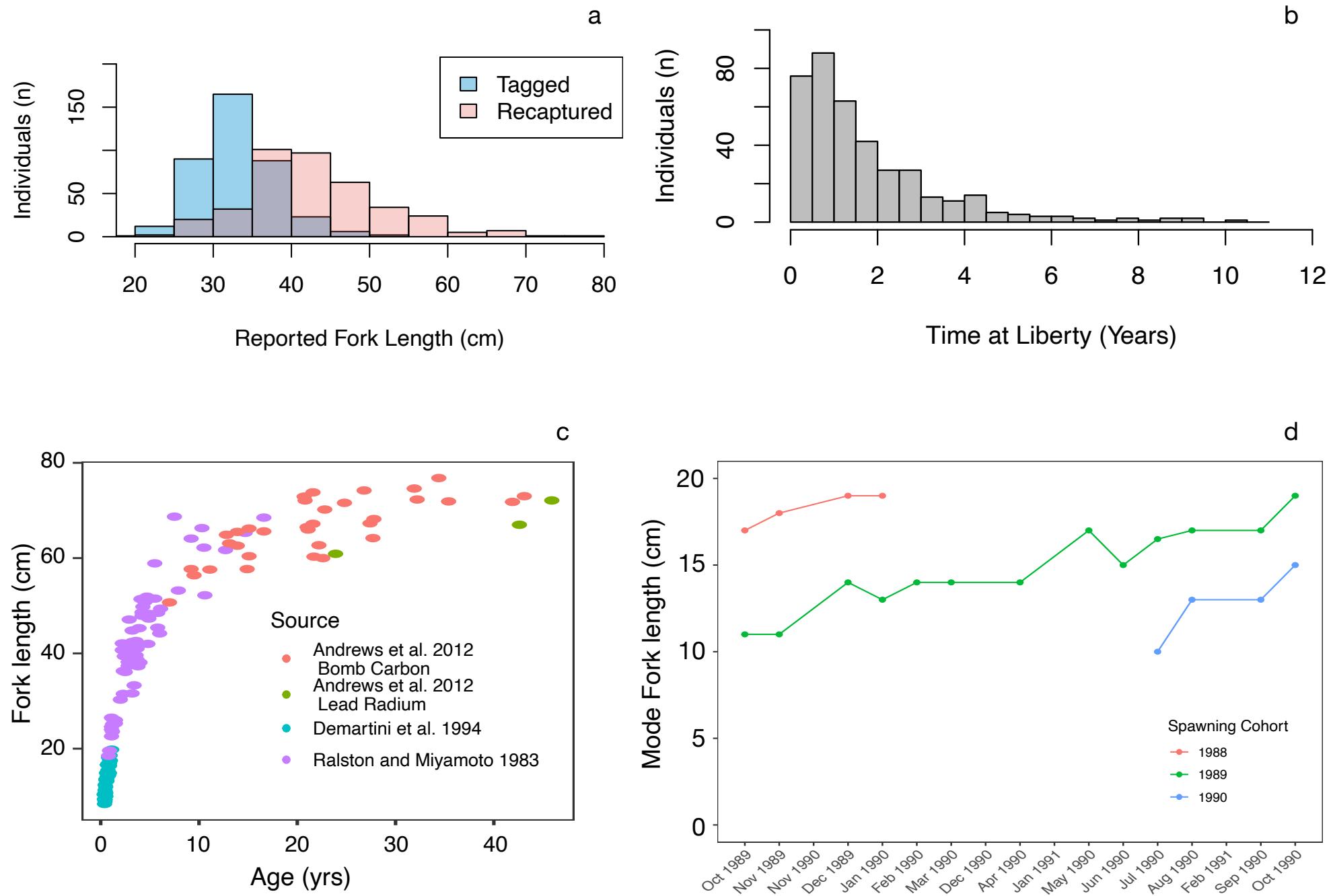


Figure 3

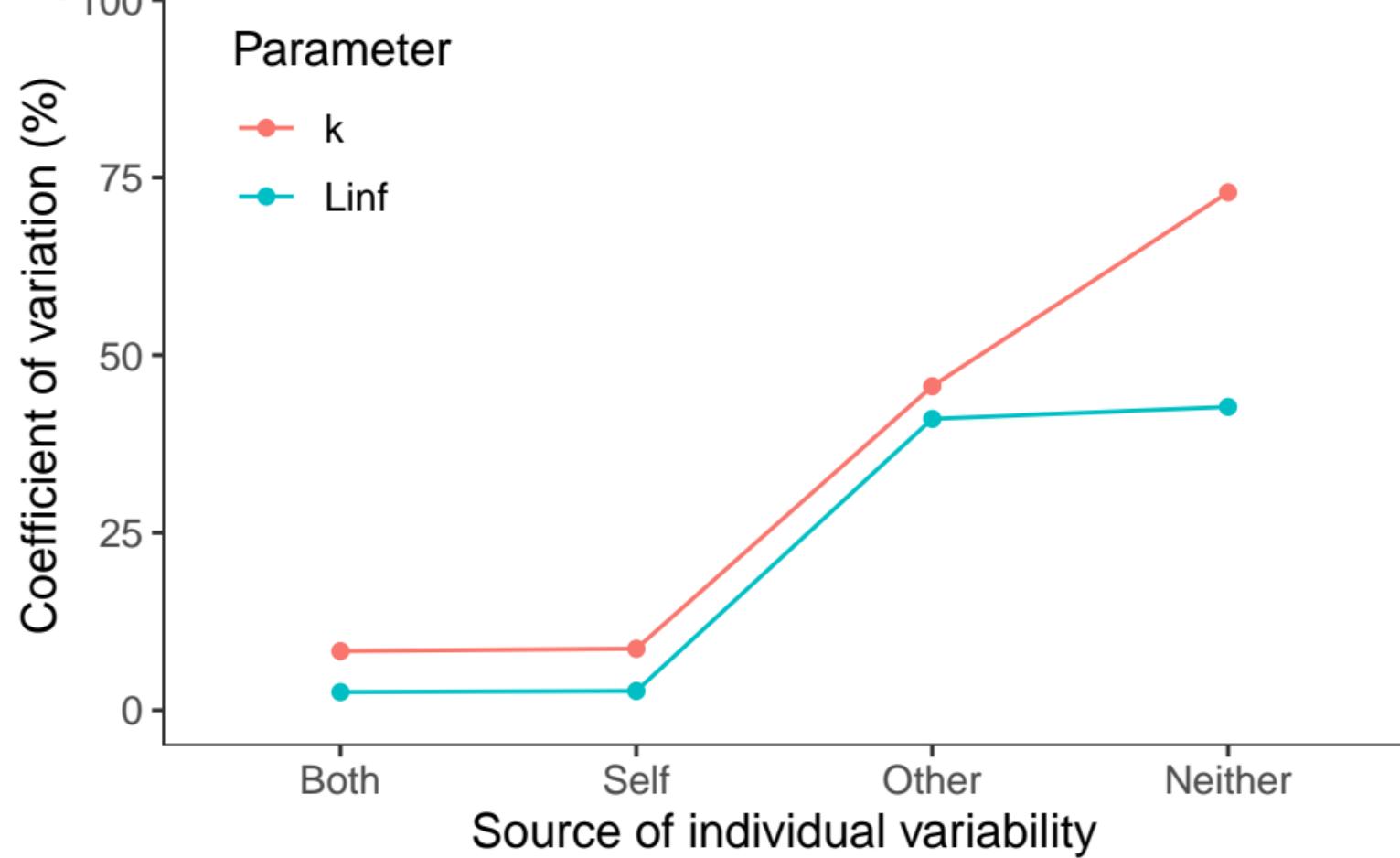
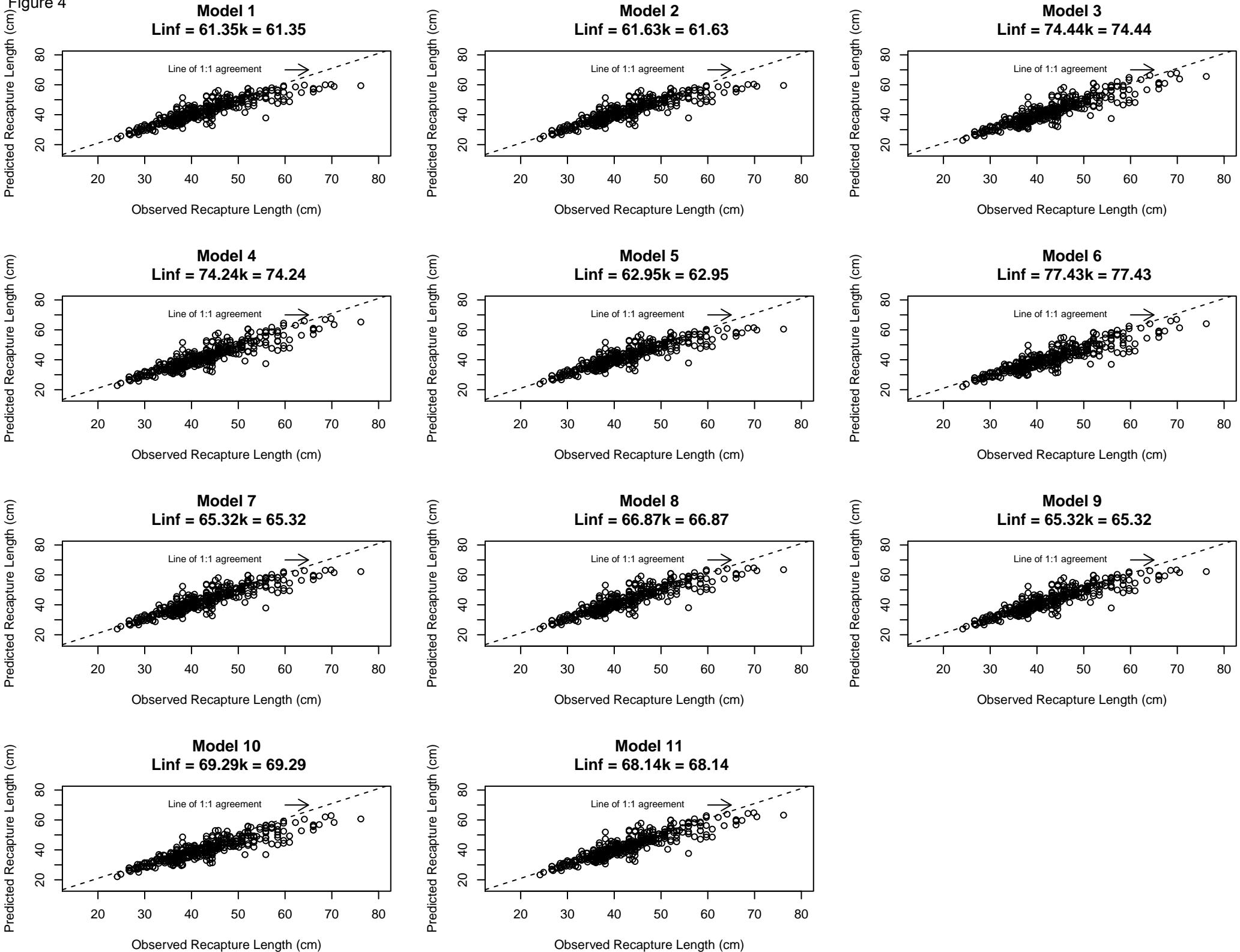


Figure 4



Stephen Scherrer: Conceptualization, Methodology, Software, Writing – Original draft, Review & Editing, Validation, Formal analysis, Visualization. **Donald Kobayashi:** Writing- Original draft, Visualization, Software. **Kevin Weng:** Resources, Writing – Review & Editing, Funding Acquisition. **Henry Okamoto:** Investigation, Data Curation. **Francis Oishi:** Investigation, Data Curation. **Erik Franklin:** Writing- Reviewing, Editing & Revision, Supervision.

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: