

Abstract.—Recent papers have provided new insights into the problem of estimating von Bertalanffy growth parameters from tag-recapture data. In particular, the inconsistency and bias of Fabens' (1965) estimates appear to have been addressed by James (1991). Using simulation, we examine the pattern of bias associated with different error assumptions for Fabens' estimates, weighted Fabens' estimates proposed by James, and a robust method also proposed by James. Our results corroborate James' finding that his robust estimates can be significantly less biased than other methods. We then apply these estimators to tag-recapture data obtained for sablefish *Anoplopoma fimbria* found in the Gulf of Alaska and off the U.S. west coast, and Pacific cod *Gadus macrocephalus* found in the eastern Bering Sea. These species are difficult to directly age, so tag-recapture data provide welcomed independent estimates of growth parameters and an indirect method of validating age-determination criteria. The von Bertalanffy parameter estimates using tag-recapture data and James' method were most similar to estimates calculated directly from length-at-age data.

Estimating von Bertalanffy growth parameters of sablefish *Anoplopoma fimbria* and Pacific cod *Gadus macrocephalus* using tag-recapture data

Daniel K. Kimura
Allen M. Shimada
Sandra A. Lowe

Alaska Fisheries Science Center, National Marine Fisheries Service, NOAA
7600 Sand Point Way NE, Seattle, Washington 98115-0070

In its most common form, the von Bertalanffy growth curve has three parameters (L_{∞} , K , t_0). Conventional interpretation of these parameters is that L_{∞} is asymptotic size, K describes the growth rate, and t_0 describes the age at length-0. Fabens (1965) was apparently the first to show how least-squares could be used to estimate two of these parameters (L_{∞} , K) from tag-recapture data. If at least one additional value of length-at-age was known, then t_0 could be estimated, and hence all values of length-at-age could be estimated directly from recapture data without recourse to direct ages from individual specimens. Besides providing growth-curve estimates, such a procedure would seem to provide an indirect validation of ageing criteria, since estimated growth parameters from length-at-age data and tag-recapture data could be compared.

However, comparisons of growth curves estimated using Fabens' method and ordinary length-at-age data seemed to provide evidence that Fabens' method provided biased parameter estimates. Following the suggestion of Chapman (1961) and others, Sainsbury (1980) showed how individual variability [i.e., the possibility that each fish has different values of (L_{∞} , K)], could lead to bias in population parameter estimates.

Francis (1988a) argued from a sampling point of view that von Bertalanffy parameters calculated from length-at-age and tag-recapture data could be different. He also argued that average growth parameters for individual fish may not describe the population growth curve (Francis 1988b). Maller & deBoer (1988) showed mathematically and with simulation that Fabens' estimates, and related estimates of Kirkwood & Somers (1984), could be inconsistent. Kirkwood (1983) suggested combining length-at-age and tag-recapture data into a single likelihood model, but did not address the problem of bias caused by the interpretation of tag-recapture data.

A recent paper by James (1991) suggests that bias in Fabens' estimates could arise from bias in the estimating functions. James shows how weighted least-squares can be used to derive improved estimates for Fabens' method under the usual "observational error" assumption. James also gives distribution-free estimates for a more general model in which, in addition to the usual observational error, L_{∞} itself is allowed to vary among individual fish. Although James' estimates appear to be consistent and less biased than the least-squares estimates, they also appear to be less efficient, usually

having larger standard errors. Nevertheless, James' method provides us with more robust parameter estimates.

This paper illustrates how critical is statistical methodology to the estimation of growth parameters from tag-recapture data. We show, by simulation and through analysis of actual data, that different estimation methods can easily lead to very different parameter estimates. With the help of simulation, we feel that realistic choices can be made among these estimators. For the actual datasets chosen for this paper, we are able to compare growth-curve parameter estimates from tag-recapture data with parameter estimates calculated from length-at-age data, using ages estimated from directly counting annuli. This provides another criterion for choosing among estimators.

Methods

We apply estimators considered by James (1991). The "unweighted Fabens" estimates (Fabens 1965) is the widely used historical method. What we call the "weighted Fabens" estimates, and James' estimates, were derived by James (1991). The weighted Fabens' method weights the residuals by an inverse variance estimate and appears to work well for the observational error model. James' estimators appear to be less prone to bias than the unweighted Fabens' estimators, and more robust to the presence of variability in L_∞ than the weighted Fabens' estimators. A more theoretical description of these estimators can be found in James (1991).

First we present a simulation study that corroborates the main findings of James (1991). Our study is more systematic than that of James (1991), using three estimation methods and error structures and calculating mean square error. Our simulation is based on parameters estimated for a marine teleost, Pacific whiting *Merluccius productus*, while James' simulations dealt with two shellfish species. Nevertheless, these simulations should be considered an addendum to James' original work.

Using notation similar to James (1991), consider a population having von Bertalanffy parameters (L_0, K_0) which we wish to estimate. L_0 refers to the average value of L_∞ in the population, where L_∞ might vary among individual fish. We assume $K=K_0$ does not vary among fish. Also, recall that t_0 cannot be estimated from tag-recapture data alone. To determine t_0 we need the average length of at least one age-group which can be supplied by direct age data (i.e., ages obtained from directly counting annuli), or the modal length-frequency of a dominant year-class of known age.

Suppose we observe the size at release (y_{1i}) and capture (y_{2i}) of $i=1, \dots, n$ fish, and the ages at release and recapture are (t_i, t_i+d_i). Suppose also that independent normally-distributed errors ($\epsilon_{1i}, \epsilon_{2i}, \epsilon_{3i}$) enter into these observations in three possible ways:

$$y_{1i} = (L_0 + \epsilon_{3i})[1.0 - \exp(-K_0 t_i)] + \epsilon_{1i}$$

$$y_{2i} = (L_0 + \epsilon_{3i})[1.0 - \exp(-K_0(t_i + d_i))] + \epsilon_{2i}$$

We refer to ϵ_{1i} and ϵ_{2i} as "observational errors" and ϵ_{3i} as "variability in L_∞ ."

The three estimators of (L_0, K_0) considered in this paper are all based on the "residuals":

$$\eta_i = y_{2i} - y_{1i} - (L_0 - y_{1i})[1.0 - \exp(-K_0 d_i)].$$

These estimators are:

- 1 Unweighted Fabens, estimated by minimizing $\sum \eta_i^2$
- 2 Weighted Fabens, estimated by minimizing $\sum [\eta_i^2 / (1.0 + \exp(-2K_0 d_i))]$.
- 3 James, estimated by solving the simultaneous equations $\sum \eta_i = 0$ and $\sum d_i \eta_i = 0$.

Unweighted and weighted Fabens' estimates, and their standard errors, were calculated using nonlinear least-squares methods. Define $g_1 = \sum \eta_i$ and $g_2 = \sum d_i \eta_i$. James' estimates were calculated as suggested by James (1991) by solving for " L_0 in terms of K_0 from g_1 followed by substitution into g_2 " and then applying the bisection method to estimate K_0 (see Press et al. 1986). This method appeared computationally robust and suitable for simulation studies. The variance estimates of these parameter estimates were calculated according to James (1991):

$$\text{cov}(\hat{L}, \hat{K}) = G^{-1} D (G^{-1})^{-1},$$

where

$$G = \begin{pmatrix} \frac{\partial g_1}{\partial K_0} & \frac{\partial g_1}{\partial L_0} \\ \frac{\partial g_2}{\partial K_0} & \frac{\partial g_2}{\partial L_0} \end{pmatrix}, \quad D = \sum \eta_i^2 \begin{pmatrix} 1.0 & d_i \\ d_i & d_i^2 \end{pmatrix},$$

and the right-hand expressions are evaluated at the estimated parameters.

Our simulation considered three different error assumptions.

Simulation 1 The observational error model where all fish are assumed to have common growth parameters, with variation due wholly to observational errors $\epsilon_{1i}, \epsilon_{2i} \sim N(0, \sigma^2)$. Here, all ϵ_{3i} are assumed to be zero.

Simulation 2 The variation in L_∞ model, where all variation in the observations are due to $\epsilon_{3i} \sim N(0, \sigma^2)$,

and all observational errors ϵ_{1i} and ϵ_{2i} are assumed to be zero.

Simulation 3 Both observational errors and variation in L_{∞} are present in this model, with ϵ_{1i} , ϵ_{2i} , $\epsilon_{3i} \sim N(0, \sigma^2)$.

For these simulations, we assume that the true population parameters are ($L_0 = 61.23$, $K_0 = 0.296$), parameters previously estimated for female Pacific whiting (Kimura 1980). Measured in years, t_{1i} and d_i were uniformly and independently distributed over the interval $[1, 5]$, assuming 365 d/yr. New values for t_{1i} and d_i were generated for every replication of the simulation.

Analytic standard errors of parameter estimates were estimated using nonlinear least-squares methods, and the variance estimate described above for James' method. In addition, the sample standard errors (i.e., the sample standard deviation of the replicate parameter estimates) are also provided. The reason for this is that the simulations included variation in t_{1i} and d_i that would not be included in the analytic estimates of standard error, and the probability that the analytic standard errors are themselves biased due to failure of assumptions. For the actual datasets, analytic standard errors were used. For simultaneously considering bias and variance, we include estimates of mean square error (MSE) calculated in the usual way: $\sum (\text{estimate} - \text{true})^2/n$.

Following a presentation of simulation results, we analyze tag-recapture data collected for sablefish *Anoplopoma fimbria* from the Gulf of Alaska and off the U.S. west coast, and Pacific cod *Gadus macrocephalus* from the eastern Bering Sea (Fig. 1). Because sablefish and Pacific cod are difficult species to directly age,

their growth-curve parameters estimated from tag-recapture data are of special interest. The von Bertalanffy parameters estimated from tag-recapture data were compared with parameters estimated from length-at-age data based on direct ages (i.e., ages from directly counting annuli). For sablefish, we use length-at-age datasets based on break and burn ages (Chilton & Beamish 1982) and parameters estimated using nonlinear least-squares (Kimura 1980). For Pacific cod, we compare tag-recapture results with published von Bertalanffy parameter estimates (Thompson & Bakkala 1990).

Results

Simulation results

For the simulation results given here, the tag-recapture sample size was $n=300$, simulations were replicated 200 times, and the normal errors (ϵ_{1i} , ϵ_{2i} , ϵ_{3i}) were all independently distributed with $\sigma^2=25$. Therefore, the sample size was realistically small and the error variances were substantial. For each estimation method and parameter, simulation results (Table 1) were summarized by four entries: sample mean of the estimated parameter, mean analytic standard error, sample standard error (i.e., the standard deviation of estimated parameters), and mean square error.

The unweighted Fabens' estimate of L_0 is biased low in Simulation 1, biased high in Simulation 2, with biases apparently canceling each other in Simulation 3. For the weighted Fabens' estimates, the L_0 estimate is unbiased for Simulation 1, but biased high for Simulations 2 and 3. James' estimate of L_0 is unbiased in Simulation 2, and only modestly biased in Simulations 1 and 3. Biases in L_0 and K_0 estimates are in the opposite direction, as might be expected from the negative correlation between these parameter estimates.

Standard errors are uniformly smallest for the unweighted Fabens' method, in the middle for the weighted Fabens' method, and largest for James' method.

Performance as measured by mean square error was entirely dependent on the assumptions of the simulation. For Simulation 1 (i.e., observational errors) the weighted Fabens' method MSE was smallest; for Simulation 2

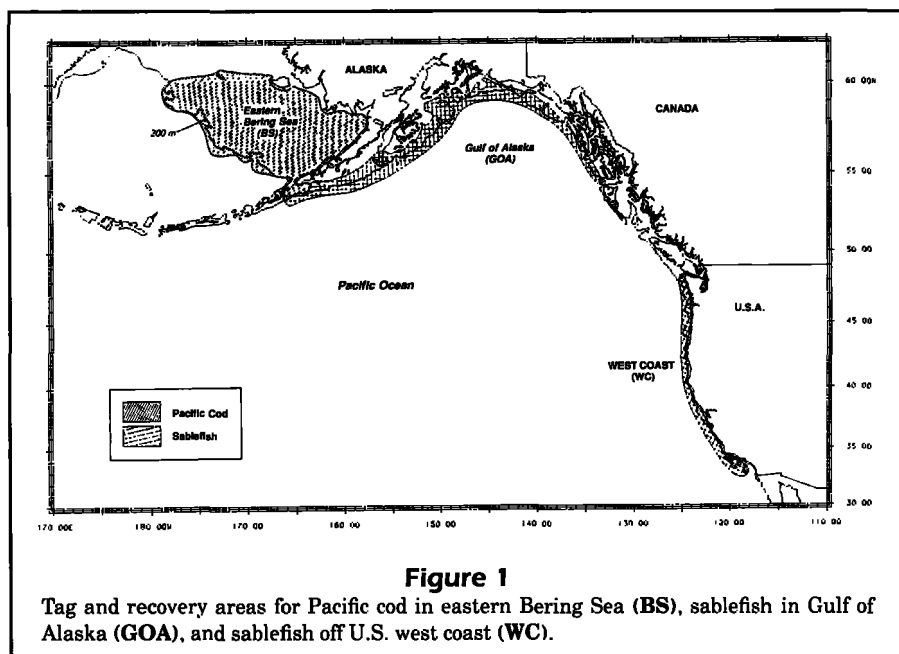


Figure 1

Tag and recovery areas for Pacific cod in eastern Bering Sea (BS), sablefish in Gulf of Alaska (GOA), and sablefish off U.S. west coast (WC).

Table 1

Simulation results using three different methods to estimate von Bertalanffy parameters ($L_0=61.23$, $K_0=0.296$) under three different error assumptions: Simulation 1 (observational error), Simulation 2 (variation in L_∞), and Simulation 3 (both observational error and variability in L_∞). For each estimation method and parameter, simulation results are summarized by four entries: sample mean of the estimated parameter, mean analytic standard error, sample standard error (i.e., standard deviation of estimated parameters), and mean square error.

Method	Parameter	Sim. 1	Sim. 2	Sim. 3
Unweighted Fabens	mean(L_0)	58.00	65.01	60.39
	mean(K_0)	0.379	0.238	0.315
	analytic SE(L_0)	1.042	0.981	1.423
	analytic SE(K_0)	0.031	0.011	0.028
	sample SE(L_0)	0.987	0.991	1.370
	sample SE(K_0)	0.030	0.012	0.026
	MSE(L_0)	11.426	15.272	2.576
	MSE(K_0)	0.00775	0.00347	0.00103
	Weighted Fabens	mean(L_0)	61.24	67.05
mean(K_0)		0.298	0.215	0.216
analytic SE(L_0)		1.355	1.154	2.347
analytic SE(K_0)		0.021	0.009	0.018
sample SE(L_0)		1.542	1.205	2.921
sample SE(K_0)		0.030	0.012	0.027
MSE(L_0)		2.365	35.347	44.197
MSE(K_0)		0.00091	0.00671	0.00714
James		mean (L_0)	62.22	61.23
	mean (K_0)	0.294	0.299	0.300
	analytic SE(L_0)	4.099	1.588	4.625
	analytic SE(K_0)	0.064	0.028	0.071
	sample SE(L_0)	4.241	1.521	5.332
	sample SE(K_0)	0.066	0.027	0.069
	MSE(L_0)	18.871	2.303	28.986
	MSE(K_0)	0.00432	0.00072	0.00471

(variability in L_∞) the James' method MSE was the smallest; for Simulation 3 (i.e., both observational error and variability in L_∞) the unweighted Fabens' method MSE was the smallest.

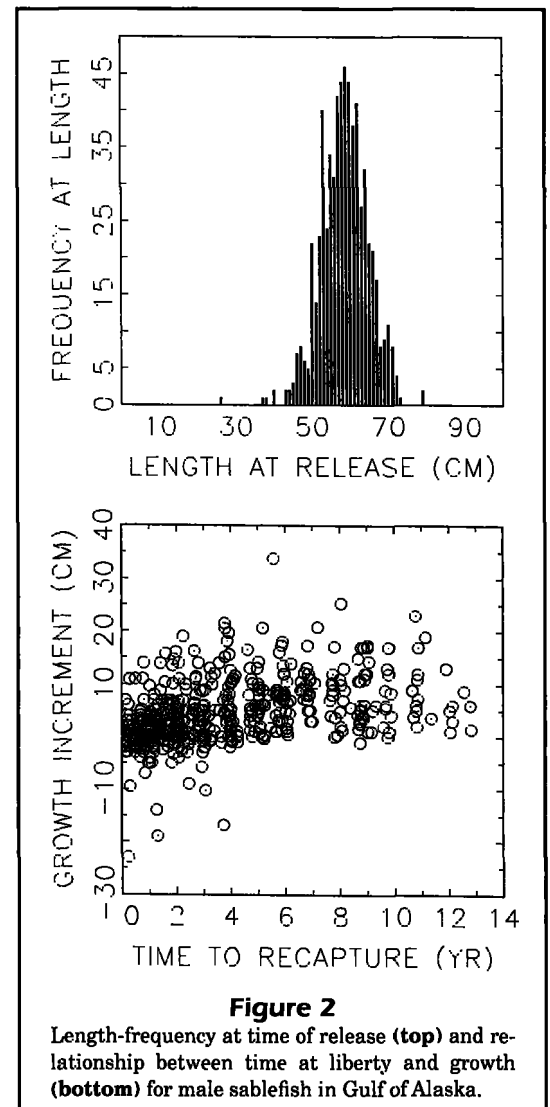
It is clear from these simulation results that unweighted or weighted Fabens' estimates of von Bertalanffy parameters can be significantly biased. It is also clear that standard errors for James' estimators tend to be larger than standard errors for the unweighted and weighted Fabens' estimators.

Estimates from sablefish tag-recapture data

Sablefish is a species characterized by rapid growth at young ages followed by extremely slow growth at older ages. In tag-recapture data, it is common for sablefish to show negative growth increments (Figs. 2,3,5,6). The exact reason for this apparent shrinkage is uncertain. However, Sasaki (1985) noted that shrinkage was usually reported for larger male (>60 cm) and female (>70 cm) sablefish. This suggests that such occurrences are due to the combined influence of slow growth and measurement error. Furthermore, Beamish & Chilton (1982) noted that the freezing of commercially-caught fish could cause

actual shrinkage. Interestingly, Beamish & Chilton (1982) also noted that data from freshly-caught fish measured by trained biologists occasionally showed shrinkage, indicating that shrinkage can occur in the ocean environment. Considering these factors, all recoveries, including those having negative growth increments, were used in the sablefish data analyses.

Although this species is extremely difficult to age (Kimura & Lyons 1991), age-determination criteria have been validated using oxytetracycline tags (Beamish & Chilton 1982) and radioisotope methods (Kastelle 1991). Because of the difficulty of directly determining ages for sablefish, estimating growth using tag-recapture data is of particular interest.

**Figure 2**

Length-frequency at time of release (top) and relationship between time at liberty and growth (bottom) for male sablefish in Gulf of Alaska.

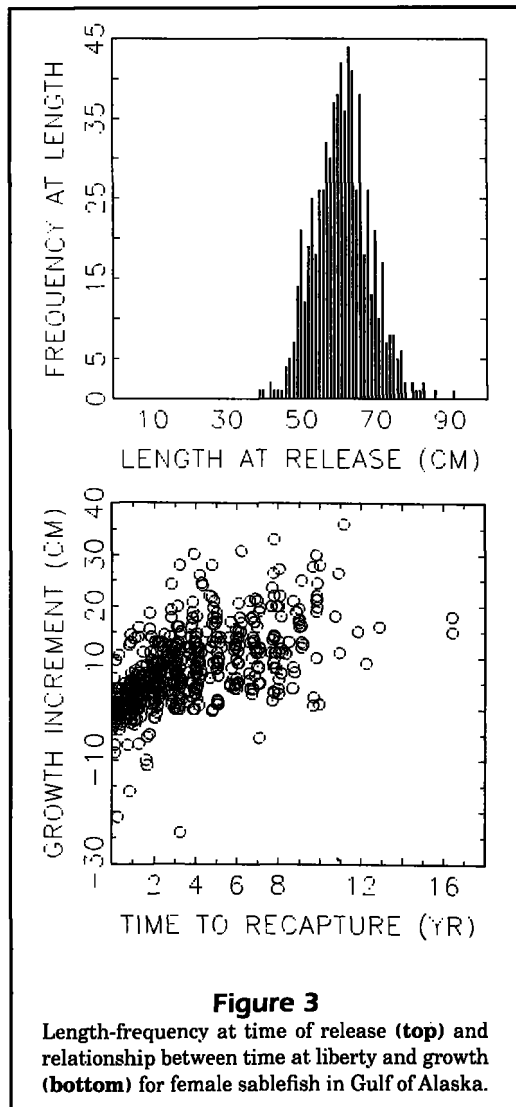


Figure 3

Length-frequency at time of release (top) and relationship between time at liberty and growth (bottom) for female sablefish in Gulf of Alaska.

Sablefish growth differs between regions, so we analyzed tag-recapture data from the Gulf of Alaska and the west coast of the United States separately (Fig. 1). Sablefish growth differs greatly by sex (Sasaki 1985), so it was necessary to estimate growth parameters for each sex.

Because the type of fishing gear used for tagging and recapture might affect the observed growth increments, we include tables of tagging and recapture gears for the usable data for all actual datasets (Table 2). Fish in the Gulf are primarily caught using longline gear, while fish off the west coast are primarily caught by trawl and pot gears.

For Gulf of Alaska sablefish, 133,558 fish were released, with 7946 recoveries between 1972 and 1990. Of these recoveries, 1340

Table 2

Cross-tabulation of release and recovery fishing gears for Gulf of Alaska sablefish, west coast sablefish, and eastern Bering Sea Pacific cod. Only tag recoveries with usable growth-increment information are included. NA = not available.

		Recovery gear				total
		NA	trawl	pot	longline	
Gulf of Alaska sablefish						
Release	NA		1		2	3
gear	trawl		2	2	28	32
	pot	5	3	17	99	124
	longline	20	81	76	1004	1181
	total	25	87	95	1133	1340
West Coast sablefish						
Release	NA	1				1
gear	trawl	14	36	8	5	63
	pot	66	464	358	68	956
	longline	12	13	31	7	63
	total	93	513	397	80	1083
Eastern Bering Sea Pacific cod						
Release						
gear	trawl	19	175	4	86	284

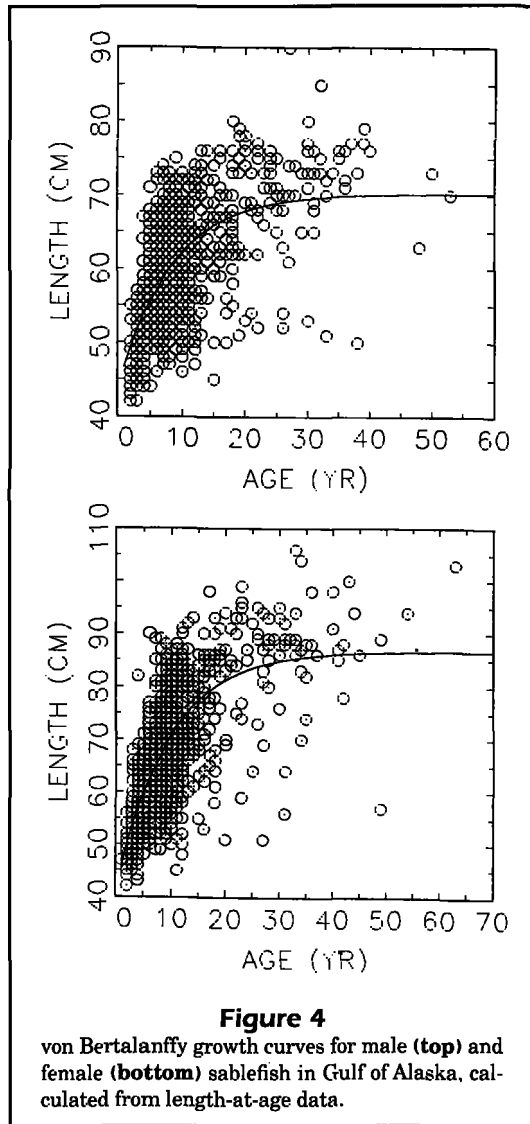
had usable growth-increment information (Figs. 2,3). Longline gear dominated both tag and recovery gears (Table 2).

Estimated von Bertalanffy parameters for sablefish in the Gulf of Alaska based on tag-recapture data can be compared with von Bertalanffy parameters estimated directly from length-at-age data (Table 3) from specimens collected on longline surveys in 1987 and 1989, and aged during 1990 and 1991 (Fig. 4). For this dataset the unweighted Fabens' estimates, the James' estimates, and estimates based on direct ages gave very similar parameter estimates. However, the weighted Fabens' estimates gave estimates quite different from the others.

Table 3

Comparison of von Bertalanffy growth parameters for sablefish in the Gulf of Alaska, estimated from tag-recapture and length-at-age data. Tag-recapture sample sizes: males $n=643$, females $n=697$. Direct-ages sample sizes: males $n=807$, females $n=1165$.

	L_0	K_0	t_0	SE(L_0)	SE(K_0)	SE(t_0)
Males						
Unweighted Fabens	70.2	0.136		0.83	0.013	
Weighted Fabens	83.0	0.049		3.43	0.007	
James	70.7	0.126		2.84	0.044	
Length-at-age	70.2	0.120	-8.06	0.95	0.014	1.17
Females						
Unweighted Fabens	83.4	0.128		1.36	0.011	
Weighted Fabens	102.8	0.055		5.02	0.007	
James	84.7	0.117		3.53	0.024	
Length-at-age	86.7	0.106	-6.15	1.22	0.008	0.62



For west coast sablefish, 52,743 fish were released, with 4220 recoveries between 1971 and 1991. Of these recoveries, 1083 had usable growth-increment information (Figs. 5,6). Pot gear was the dominant release gear, but both trawl and pot were important recovery gears (Table 2).

Estimated von Bertalanffy parameters for west coast sablefish based on tagging data can be compared with von Bertalanffy parameters estimated directly from length-at-age data (Table 4) from specimens collected in trawl and pot surveys in 1983 and 1989, and aged during 1991 and 1992 (Fig. 7). For this dataset, only James' estimates compared well with estimates based on direct ages. If James' estimates were not available, we could

not conclude that estimates of growth parameters based on tagging were consistent with length-at-age data generated by age readers. Unexpectedly for the west coast dataset, James' estimates of $SE(L_0)$ were smaller than for the unweighted Fabens' estimates.

Another possible problem when analyzing growth-increment data is that the observed increments may be dependent on the tag or recovery gears that are used. Our west coast sablefish tag-recapture dataset provides an opportunity to examine whether observed growth increments may depend on the fishing gears used for tagging and recapture. From this dataset, we selected only fish with pot gear releases and trawl or pot gear recoveries. We then regressed growth increment against sex, recovery gear, size-at-release, and time at liberty. The analysis showed that fish recovered by pot gear could be expected to have growth increments 3.7 cm larger (significant $\alpha=0.0001$) than fish recovered by trawl gear after the other independent variables were taken into account. Thus, release and recovery gears can be expected to affect the growth curves estimated from tag-recapture data.

Estimates from Pacific cod tag-recapture data

Pacific cod has also proved to be a very difficult species to directly age (Kimura & Lyons 1990). For eastern Bering Sea (Fig. 1) Pacific cod, 12,396 tagged fish were released, with 375 recoveries between 1982 and 1989. Of these recoveries, 284 had usable growth-increment information (Fig. 8). Bottom trawl was the only release gear, but both trawl and longline were important recovery gears (Table 2). Because of the small tag-recapture sample size available for Pacific cod, we combined male and female data into a single fit.

As with sablefish, Pacific cod tag recaptures can show negative growth increments (Fig. 8). For the complete tag-recapture dataset, unweighted and weighted Fabens' estimates were biased when compared with estimates based on length-at-age data (Table 5). James' estimates did not exist within a reasonable range for K_0 ($0.01 < K_0 < 1.0$). Using recoveries with only positive growth increments allowed James' estimates to be close to those based on length-at-age data (Table 5). After deleting only the larger negative growth increments (i.e., larger in absolute value), data with increments greater than -10 cm gave a standard error for L_0 using James' method of 53.4 cm. These results indicate that for James' estimates, the sample size for Pacific cod was insufficient to overcome variability in the data.

Discussion

Our simulation study confirmed that James' robust estimators for estimating von Bertalanffy parameters from tag-recapture data show little bias when variability can be described by simple observational error and/or variability in L_∞ . In contrast, the unweighted and weighted Fabens' estimators sometimes had

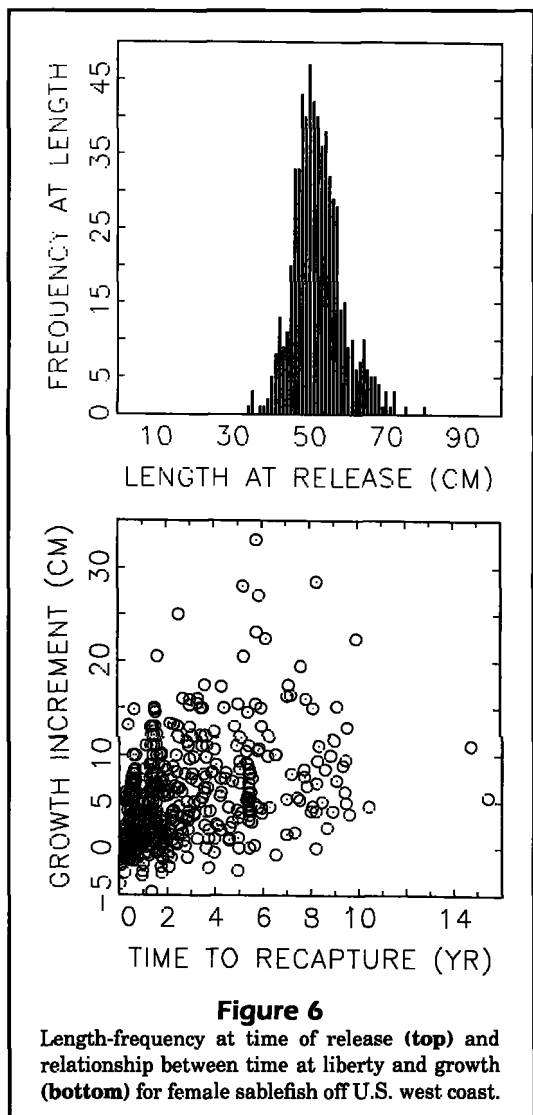
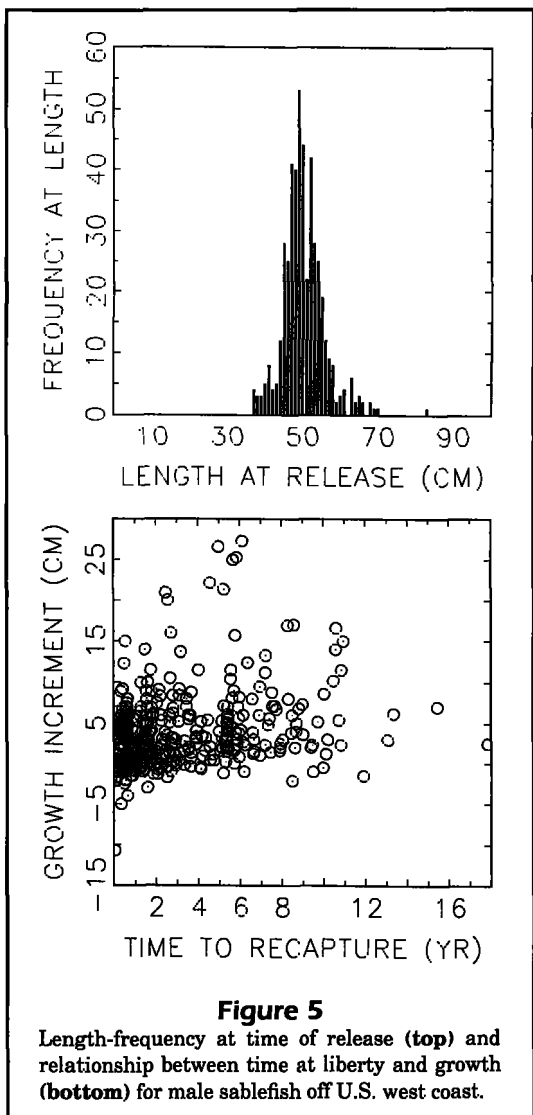


Figure 5

Length-frequency at time of release (top) and relationship between time at liberty and growth (bottom) for male sablefish off U.S. west coast.

Figure 6

Length-frequency at time of release (top) and relationship between time at liberty and growth (bottom) for female sablefish off U.S. west coast.

Table 4

Comparison of von Bertalanffy growth parameters for sablefish off the U.S. west coast, estimated from tag-recapture and length-at-age data. Tag-recapture sample sizes: males $n=467$, females $n=616$. Direct-ages sample sizes: males $n=714$, females $n=814$.

	L_0	K_0	t_0	$SE(L_0)$	$SE(K_0)$	$SE(t_0)$
Males						
Unweighted Fabens	65.4	0.081		2.08	0.014	
Weighted Fabens	144.2	0.009		100.2	0.010	
James	56.6	0.556		0.65	0.108	
Length-at-age	54.7	0.472	-1.82	0.23	0.055	0.51
Females						
Unweighted Fabens	71.5	0.110		1.79	0.013	
Weighted Fabens	130.1	0.020		33.2	0.008	
James	61.4	0.481		0.92	0.085	
Length-at-age	61.0	0.499	-0.81	0.35	0.047	0.32

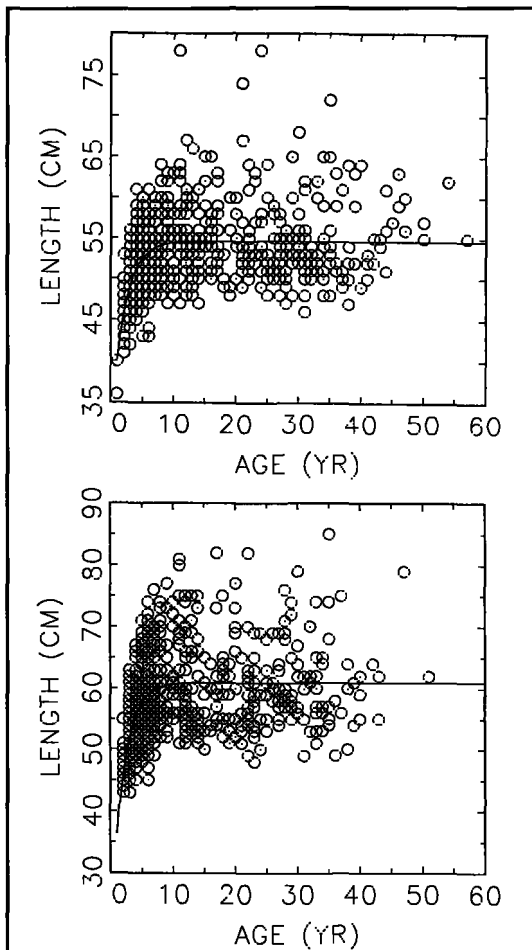


Figure 7
von Bertalanffy growth curves for male (top) and female (bottom) sablefish off U.S. west coast, calculated from length-at-age data.

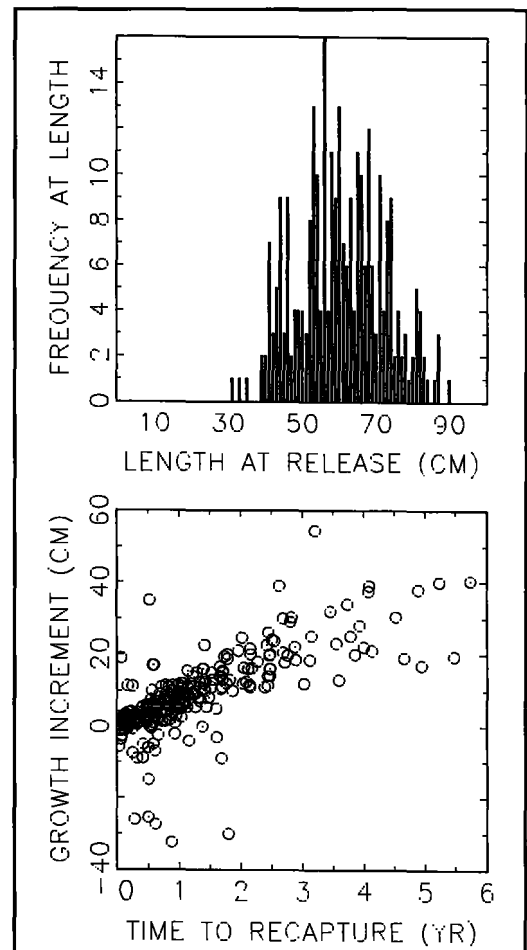


Figure 8
Length-frequency at time of release (top) and relationship between time at liberty and growth (bottom) for Pacific cod in eastern Bering Sea.

Table 5

Comparison of von Bertalanffy growth parameters for Pacific cod in eastern Bering Sea, estimated from tag-recapture data using all growth increments ($n=284$), only positive growth increments ($n=252$), and length-at-age data. Sexes were combined, and von Bertalanffy parameters estimated from length-at-age data were taken from Thompson & Bakkala (1990). NS = no solution, NA = not available.

	L_0	K_0	t_0	SE(L_0)	SE(K_0)	SE(t_0)
All growth increments						
Unweighted Fabens	117.0	0.148		9.69	0.029	
Weighted Fabens	271.0	0.035		147.81	0.024	
James	NS	NS		NS	NS	
Positive growth increments						
Unweighted Fabens	126.3	0.133		8.35	0.020	
Weighted Fabens	175.1	0.070		28.19	0.017	
James	104.3	0.222		10.55	0.065	
Length-at-age	105.4	0.237	1.06	NA	NA	NA

large biases. However, the standard errors for James' estimators tended to be larger, so in terms of mean square error the superior estimation method depended on the assumptions we made concerning variability.

Weighted Fabens' estimators performed well when error was restricted to observational error, but were badly biased when variability in L_{∞} was introduced into the simulation. In contrast, James' estimators performed well when there was no observational error and error was due only to variability in L_{∞} . The unweighted Fabens' estimators were biased when error was solely observational, and biased when variability was due solely to variability in L_{∞} , but biases apparently canceled when both errors were present.

It is difficult to recommend the unweighted or weighted Fabens' estimators because they are both subject to large biases. It seems difficult to assume biases will cancel, or that there will be no variability in the data due to variability in L_{∞} .

On the other hand, the James' estimators appeared unbiased but tended to have larger standard errors. Our experience with analyzing the small sample-size dataset available for Pacific cod indicates that James' estimators may require at least moderate sample sizes, the required size depending on variability in the data. If sample sizes are sufficiently large, reducing bias can be far more important than increasing efficiency. Therefore, it seems important that James' estimators be used to at least guard against possible biases. More experience with James' method will probably be needed before researchers can finally decide the correct scope of application for this new method.

In this paper we have used von Bertalanffy parameter estimates based on direct ages as the yardstick by which to measure bias for the three different estimators. Of course, von Bertalanffy parameter estimates based on length-at-age data might themselves be biased. Except for the small sample-size dataset available for Pacific cod, James' estimators compared well with estimates based on direct age data. Unweighted Fabens' estimators compared well with estimates based on direct ages for one dataset. Weighted Fabens' estimators of L_0 appeared to be biased high for all three datasets.

This pattern of bias suggests that the tag-recapture data in these actual datasets contain significant amounts of variability due to variability in L_{∞} . This is also evidenced by the length-at-age data (see Figs. 4,7). For the three stocks of fish studied in this paper, we conclude that there are no inconsistencies in growth described by direct ages and growth described by tag-recapture data. Without James' estimators, this conclusion could not be made. We feel that James' method represents a significant step forward, and that datasets

previously analyzed using Fabens' method might benefit by being reexamined using James' method. However, results may be the same as Fabens' estimates, or quite different, depending upon the nature of variability in the data.

Still, problems remain when evaluating growth from tag-recapture data. McFarlane & Beamish (1990) concluded that external tags could markedly affect the growth of sablefish. We have shown that different fishing gear types may select for slower- or faster-growing individuals. For the west coast sablefish tag-recapture datasets, growth increments appeared larger for fish recovered with pot gear compared with trawl gear. Therefore, sampling gears always play a role in describing the growth parameters we estimate.

Acknowledgments

We thank R.A. Maller, an anonymous referee, and the editorial staff of the journal for comments that greatly facilitated our revision. We thank F.R. Shaw for providing access to the sablefish tag-recovery database. This study was motivated by original insights into tag-recapture growth parameter estimation from I.R. James.

Citations

Beamish, R. J., & D. E. Chilton

1982 Preliminary evaluation of a method to determine the age of sablefish (*Anoplopoma fimbria*). *Can. J. Fish. Aquat. Sci.* 39:277-287.

Chapman, D. G.

1961 Statistical problems in dynamics of exploited fish populations. *Proc. Berkeley Symp. Math. Stat. Probab.* 4:153-168.

Chilton, D. E., & R. J. Beamish

1982 Age determination methods for fishes studied by the Groundfish Program at the Pacific Biological Station. *Can. Spec. Publ. Fish. Aquat. Sci.* 60:1-102.

Fabens, A. J.

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

Francis, R. I. C. C.

1988a Are growth parameters estimated from tagging and age-length data comparable? *Can. J. Fish. Aquat. Sci.* 45:936-942.

1988b Maximum likelihood estimation of growth and growth variability from tagging data. *N.Z. J. Mar. Freshwater Res.* 22:42-51.

James, I. R.

1991 Estimation of von Bertalanffy growth curve parameters from recapture data. *Biometrics* 47:1519-1530.

Kastelle, C. R.

1991 Radioisotope age validation and an estimate of natural mortality from the gonad to somatic weight index for sablefish (*Anoplopoma fimbria*). M.S. thesis, Univ. Wash., Seattle, 87 p.

Kimura, D. K.

1980 Likelihood estimates for the von Bertalanffy growth curve. Fish. Bull., U.S. 77:765-776.

Kimura, D. K., & J. J. Lyons

1990 Choosing a structure for the production ageing of Pacific cod (*Gadus macrocephalus*). Int. N. Pac. Fish. Comm. Bull. 50:9-23.

1991 Between-reader bias and variability in the age-determination process. Fish. Bull., U.S. 89:53-60.

Kirkwood, G. P.

1983 Estimation of von Bertalanffy growth curve parameters using both length increment and age-length data. Can. J. Fish. Aquat. Sci. 40:1405-1411.

Kirkwood, G. P., & I. F. Somers

1984 Growth of two species of tiger prawn, *Penaeus esculentus* and *P. semisulcatus*, in the western Gulf of Carpentaria. Aust. J. Mar. Freshwater Res. 35:703-712.

Maller, R. A. & E. S. deBoer

1988 An analysis of two methods of fitting the von Bertalanffy curve to capture-recapture data. Aust. J. Mar. Freshwater Res. 39:459-466.

McFarlane, G. A., & R. J. Beamish

1990 Effect of an external tag on growth of sablefish (*Anoplopoma fimbria*) and consequences to mortality and age at maturity. Can. J. Fish. Aquat. Sci. 47:1551-1557.

Press, W. H., B. P. Flannery, S. A. Teukolsky, & W. T. Vetterling

1986 Numerical recipes (the art of scientific computing). Cambridge Univ. Press, 818 p.

Sainsbury, K. J.

1980 Effects of individual variability on the von Bertalanffy growth equation. Can. J. Fish. Aquat. Sci. 37:241-247.

Sasaki, T.

1985 Studies on the sablefish resources in the North Pacific Ocean. Bull. Far Seas Fish. Res. Lab. 22:1-108.

Thompson G. G., & R. G. Bakkala

1990 Assessment of the eastern Bering Sea Pacific cod stock using a catch-at-age model and trawl survey. Int. N. Pac. Fish. Comm. Bull. 50:215-236.