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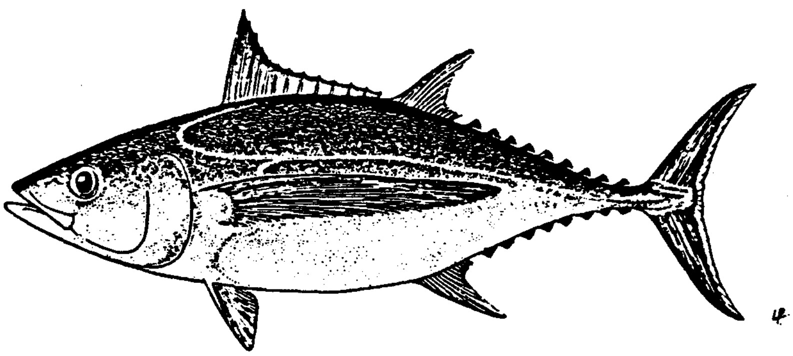

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MULTIFAN Analysis of South Pacific Albacore Length-Frequency Data Collected by Observers, 1988-89 and 1989-90

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Introduction

Otolith increment counts and limited length-increment data obtained from tag returns have previously been used to infer the age and growth of South Pacific albacore (Wetherall et al. 1989). These data have produced inconsistent results, in particular for their interpretation in relation to length-frequency data. The four tag returns received to date with usable recovery length data had average growth rates of 0.55, 0.59, 0.60 and 0.73 cm mo^{-1} for fish ranging in size from 72 to 80 cm at release. These data are consistent with the interpretation that the three commonly seen modes in length-frequency data from the troll fishery represent annual cohorts (the spacing between the second and third of these modes is about 8 cm). On the other hand, a study of South Pacific albacore age and growth using presumed daily otolith increments suggested that the growth rate was substantially higher - about 1.32 cm mo^{-1} for albacore 70-80 cm long and 1.17 cm mo^{-1} for albacore 80-90 cm long (Wetherall et al. 1989). These growth rates are consistent with the modes seen in length-frequency data being 6 mo apart rather than 1 yr.

The differing interpretations of albacore growth have a substantial effect on stock assessment. Faster growth would suggest younger spawning, higher natural mortality, faster turnover of the population and greater resilience to exploitation than the alternative growth hypothesis (Hampton 1989). Furthermore, the faster growth hypothesis would imply that potential yields are substantially greater, and that yield-per-recruit considerations would favour exploitation of smaller fish on average than under the alternative hypothesis.

Which of the interpretations of albacore growth is correct? The tag returns are presently insufficient for analyses of the data to provide conclusive results. On the other hand, the growth rates suggested by the daily otolith increment work provide a somewhat radical interpretation of the length-frequency data - such clearly defined semestral spawning, which would be necessary to produce biannual cohorts of this nature, would be unique as far as tuna are concerned. In fact, the existing evidence from larval survey work suggests that most tunas spawn during the summer months, with the spawning season being protracted for the predominantly tropical tunas (skipjack, yellowfin, bigeye) and more contracted for the species with temperate distributions (albacore, northern and southern bluefin).

It is potentially possible to derive information on growth rate from the length-frequency data themselves, particularly when well-formed modes are clearly visible, as is the case for albacore. Several statistical techniques are available for this purpose, most of which are based on the disaggregation of the length-frequency distributions into normal or log-normal components that are assumed to represent cohorts. The newest technique is called MULTIFAN (Fournier et al. 1990), which has the attractive advantage of being able to systematically test different hypotheses relating to growth and the structure of the length-frequency data. MULTIFAN processes a time-series of length-frequency samples simultaneously, using within-sample information on the spacing of modes and between-sample information on modal progression to estimate the growth-related parameters of the model.

In this paper, MULTIFAN is used to estimate von Bertalanffy growth and related parameters from a time-series of nine monthly length-frequency samples collected by observers during the 1988-89 and 1989-90 South Pacific albacore troll fisheries. Fits to the data assuming annual and biannual cohort frequencies are compared.

Length-Frequency Data

The length-frequency data used in this study were collected by observers on United States and New Zealand troll vessels operating in the subtropical convergence zone of the South Pacific Ocean (35-40°S, 130-160°W) during the 1988-89 and 1989-90 fishing seasons. Detailed descriptions of the albacore observer programme in these seasons are given in Hampton et al. (1989) and Hampton and Murray (1990).

Albacore were sampled in the subtropical convergence zone on board three troll vessels from December 1988 to April 1989 and on board six vessels from January to April 1990. Length-frequency data collected from troll vessels in the Tasman Sea and in New Zealand coastal waters were not used in this analysis to avoid any complications that might result from possible geographical variation in growth rates or recruitment.

The observers generally attempted to measure all fish caught during a day's fishing, although occasionally this was not possible due to high catch rates. This resulted in very large sample sizes - the total number of albacore measured per month ranged from 351 to 23,250 (Table 1). Fork length was measured from the tip of the snout with the mouth closed to the end of the median caudal fin ray and rounded down to the next whole centimeter.

Table 1. **Numbers of boat days sampled and numbers of albacore measured, by month.**

Month	No. boat days	No. albacore measured	No. albacore per boat day
Dec 88	2	351	175
Jan 89	28	6,017	215
Feb 89	9	1,520	169
Mar 89	10	649	65
Apr 89	13	2,022	156
Jan 90	26	10,423	401
Feb 90	56	20,608	368
Mar 90	73	23,250	318
Apr 90	22	6,959	316
Total	239	71,799	300

To maximize the catch of higher value, larger albacore, it was general practice on all vessels sampled to release live, undamaged albacore smaller than about 55 cm. Released albacore could not be measured; only the small fish that were damaged in the catching process were retained and could be measured. This resulted in biased sampling of the first cohort present in the data. Fortunately, MULTIFAN is able to accommodate, and in fact estimate, this bias.

The nine monthly length-frequency samples (with the best-fitting annual-cohort model indicated) are shown in Figure 1.

The MULTIFAN Model

A detailed description of the mathematical basis of the MULTIFAN model is given in Fournier et al. (1990). Only detail necessary to describe the strategy adopted in fitting the models is presented here.

MULTIFAN systematic searches

One problem with nonlinear parameter estimation is the possibility of the existence of multiple minima of the objective function. If the search for possible fits to the data does not cover a large enough region of parameter space, a local minimum of the objective function may be mistakenly accepted as a global minimum. To reduce the probability of incorrectly accepting a local minimum, the parameter space is partitioned into partially overlapping subregions and the log-likelihood function is minimized within each subregion. This search procedure, which forms the fundamental organisational unit of a MULTIFAN analysis, is called a systematic search.

Each systematic search is associated with a particular structural hypothesis relating to the length-frequency data. The initial systematic search is associated with the simplest model structure - the mean lengths-at-age lie (more or less) on a von Bertalanffy growth curve and the standard deviation of lengths-at-age is the same for all cohorts. A crucial piece of information that MULTIFAN (or any other method of length-frequency analysis) cannot estimate directly is the number of significant cohorts present in the data. This difficulty is accommodated by fitting the model to the data over a plausible range of significant cohorts, specified by the user, then using statistical theory to decide the number of cohorts that can be justifiably included in the model. This is done by calculating the maximum value of the log-likelihood function, first for the smallest number of cohorts specified, then for successively larger numbers of cohorts through the user-specified range. For each additional cohort included, the maximum log-likelihood function value will increase, and χ^2 tests are used to determine what constitutes a significant increase. The 0.90 point on the χ^2 distribution is taken as the critical point for acceptance or rejection of an extra cohort. This point is used instead of the traditional 0.95 point because simulations have shown that growth parameter estimates are more sensitive to underestimation of the number of significant cohorts than to overestimation (Rosenberg and Beddington 1987).

In addition to number of cohorts, each systematic search is also carried out over a user-specified range of initial estimates of the von Bertalanffy growth parameter K. This is done to ensure that the parameter space is fully searched thus reducing the probability that a local minimum will be incorrectly accepted as a global minimum.

Thus, for a given model hypothesis, a systematic search is a two-dimensional grid search for the best model fit, with the dimensions of the grid being number of significant cohorts in the data and initial estimates of K. On the basis of the maximum log-likelihood values obtained for each member of the grid and the hypothesis tests relating to the number of cohorts, a single fit from the systematic search, and the set of parameter estimates associated with it, can be identified as the best fit. Different hypotheses may then be added to the model, and the best fits from these systematic searches compared with each other using statistical tests similar to that described above. The selection of the best-fitting model across all systematic searches is complicated by the fact that the number of significant cohorts in the data can change with the addition of various structural hypotheses. MULTIFAN chooses the "best-fitting" model by comparing all fits for all systematic searches. Models with the same structural hypotheses but different numbers of cohorts are compared using the 0.90 point on the χ^2 distribution as the acceptance/rejection criterion, as noted above. However, the criterion for acceptance of additional structural hypotheses was the 0.95 point on the χ^2 distribution, regardless of the number of significant cohorts deemed to be present.

Structural hypotheses

The structural hypotheses that were tested for the albacore length-frequency data were:

(1) Basic systematic search (simplest model structure)
(2) Sampling bias in the first cohort (SB)
(3) Age-dependent standard deviation in length-at-age (ADSD)
(4) Seasonality in growth (SG)

The hypothesis of **sampling bias in the first cohort** recognises the possibility of, amongst other things, size-dependent selection against small fish by the fishing gear. The practice of releasing small albacore without measuring them could also generate such a bias. If significant sampling bias exists but is not incorporated into the model, the apparent mean length of the first cohort will be higher that that of the population at large because only the larger members of the cohort are sampled. This can have profound effects on MULTIFAN parameter estimates and in particular can result in severe under-estimates of *K*. Under this hypothesis, it is assumed that size selective bias only occurs for the first are class and that it decreases linearly with age until fish reach the second cohort.

For many fish populations, the standard deviation of length-at-age does not remain constant with age, but seems to vary in a regular fashion. Most commonly, the standard deviation of length-at-age increases with age, resulting possibly from individual variation in growth. The hypothesis of **age-dependent standard deviation in length-at-age** models this process as a simple linear function, with the standard deviations either increasing or decreasing with age.

The hypothesis of **seasonal growth** is incorporated in the form proposed by Pauly and Gaschütz (1979). This hypothesis adds two parameters to the model, one representing the magnitude of the seasonal effect and the other determining the months where the seasonal component of the growth rate reaches its maximum and minimum values.

A strategy was adopted for incorporating each of these hypotheses into the MULTIFAN systematic searches such that all possible combinations of the three structural hypotheses additional to the basic systematic search were tested. The systematic searches were:

Systematic search 1: Basic systematic search
Systematic search 2: Basic systematic search + SB
Systematic search 3: Basic systematic search + ADSD
Systematic search 4: Basic systematic search + SG
Systematic search 5: Basic systematic search + SB + ADSD
Systematic search 6: Basic systematic search + SB + SG

Systematic search 7: Basic systematic search + ADSD + SG
Systematic search 8: Basic systematic search + SB + ADSD + SG

Annual or biannual cohorts?

In its standard format, MULTIFAN assumes that the modes in the length-frequency data are the result of annual cohorts. As stated earlier, an objective of this study was to test whether this assumption, or that of biannual cohorts, provides the better fit to the data. There is currently no elegant way to do this, as MULTIFAN is designed to accommodate annual cohorts only. However, a procedure was devised that would be identical to MULTIFAN assuming biannual cohorts. This procedure involved renumbering the samples from one per month to one per two months (Table 2). The only other adjustment necessary is to double the estimated values of *K* to make them equivalent to those derived from the monthly samples. Systematic searches in which annual cohorts are assumed are denoted by A and those in which biannual cohorts are assumed are denoted by B, e.g. the systematic search that includes sampling bias in the first cohort and assumes annual cohorts is denoted A2.

Table 2. Numbering of samples for assumed annual and biannual cohorts.

Sample No.	Month/year	Year/month number	
		Annual cohorts	Biannual cohorts
1	Dec 88	1/1	1/1
2	Jan 89	1/2	1/3
3	Feb 89	1/3	1/5
4	Mar 89	1/4	1/7
5	Apr 89	1/5	1/9
6	Jan 90	2/2	3/3
7	Feb 90	2/3	3/5
8	Mar 90	2/4	3/7
9	Apr 90	2/5	3/9

Results

Annual cohorts

The results of the best fits for systematic searches that assumed annual cohorts are summarised in Table 3.

Table 3. Best fits to albacore length-frequency data for MULTIFAN systematic searches that assumed annual cohorts.

Parameter	Systematic search							
	A1	A2 SB	A3 ADSD	A4 SG	A5 SB ADSD	A6 SB SG	A7 ADSD SG	A8 SB ADSD SG
K (yr^{-1})	0.075	0.312	0.068	0.280	0.293	0.300	0.088	0.280
L_∞ (cm)	181.9	98.9	192.5	93.9	101.7	99.6	163.4	102.0
No. cohorts	5	7	5	9	6	7	5	6
First length (cm)	58.73	55.64	58.54	59.59	55.25	57.35	59.41	57.28
Last length (cm)	90.63	92.23	90.51	90.22	90.98	92.65	90.15	90.98
Age of 1st cohort (yr)	5.20	2.65	5.32	3.60	2.67	2.85	5.16	2.95
Sampling bias month 1 (cm)		3.457			3.634	3.106		2.820
Av. sd (cm)	2.413	2.285	2.533	2.013	2.442	2.230	2.459	2.372
First sd/ last sd			1.652		1.496		1.721	1.557
Seasonal growth								
Amplitude				0.939		0.943	0.949	0.928
Phase (mo)				0.339		0.398	0.360	0.391
No. Parameters	40	59	41	78	51	61	43	53
Log-likelihood	11646.1	11721.3	11699.9	11881.9	11749.8	11908.7	11887.5	11950.8

The addition of each of the structural hypotheses resulted in a significant increase in the log-likelihood, with seasonal growth providing the largest increase. Using the method of best-fit selection outlined earlier, the model including all three structural hypotheses was selected (A8 in Table 3). The fit of this model to the length-frequency data is displayed in Figure 1; there are no serious anomalies between the observed and predicted frequencies.

Biannual cohorts

The same model-fitting and model-selection procedures were also applied to the data assuming biannual cohorts. The results of the best fit for each systematic search are shown in Table 4. The introduction of sampling bias in the first cohort did not result in a significant improvement in the log-likelihood for systematic searches B2, B5 or B8. The hypothesis of age-dependent standard deviations did significantly improve the log-likelihood, as did that pertaining to seasonal growth. The best-fitting model in systematic search B7 was chosen as the most appropriate for the data assuming biannual cohorts. The fit of this model is shown in Figure 2.

Table 4. **Best fits to albacore length-frequency data for MULTIFAN systematic searches that assumed biannual cohorts.**

Parameter	Systematic search							
	B1	B2 SB	B3 ADSD	B4 SG	B5 SB ADSD	B6 SB SG	B7 ADSD SG	B8 SB ADSD SG
K (yr^{-1})	0.496	0.536	0.188	0.538	0.134	0.418	0.172	0.172
L_∞ (cm)	96.9	94.5	155.1	94.4	189.8	109.3	165.0	165.0
No. cohorts	9	9	6	9	5	6	5	5
First length (cm)	57.52	57.46	57.32	57.43	57.43	56.29	57.29	57.29
Last length (cm)	91.47	90.16	93.86	90.12	88.61	90.61	88.54	88.54
Age of 1st cohort (yr)	1.81	1.75	2.46	1.75	2.68	1.73	2.49	2.49
Sampling bias month 1 (cm)		0.000			0.000	1.377		0.000
Av. sd (cm)	2.068	2.059	2.485	2.048	2.422	2.216	2.415	2.415
First sd/ last sd			1.641		1.612		1.669	1.669
Seasonal growth								
Amplitude				0.114		0.394	0.314	0.314
Phase (mo)				-0.114		-0.236	-0.196	-0.196
No. Parameters	76	77	50	78	42	52	43	44
Log-likelihood	11846.1	11745.7	11815.4	11851.4	11819.7	11819.6	11853.0	11853.0

Comparison between annual- and biannual-cohort models

There are various ways to compare the annual- and biannual-cohort models. The simplest is to compare the best fitting annual model (A8) with the best-fitting biannual model (B7). Model A8 has a log-likelihood of 11,950.8 with 53 parameters, while model B7 has a log-likelihood of 11,853.0 with 43 parameters. Our null hypothesis (H_0) is that the simpler model (B7) is the correct model against the alternative hypothesis (H_a) that model A8 is correct. The χ^2 value for this test is 97.8 with 10 degrees of freedom. On this basis, H_0 is rejected in favour of H_a (P>0.999), therefore the annual model is favoured.

The time series of samples connected by the growth curves for these models are shown in Figure 3. Notice that the modes between years are connected in a different fashion for the two models. Growth curves derived from the two models are shown in Figure 4. More rapid growth is displayed by the biannual model, and growth is nearly linear over the observed size range.

Fits to the annual and biannual models for other combinations of structural hypotheses may also be compared from Tables 3 and 4. It is apparent that annual models fit the data better than biannual models only when seasonal growth is included. In all other cases, the biannual models provide the better fit, both when the best-fitting biannual models (Table 4) and the biannual models with the same number of significant cohorts as the best-fitting annual models (Table 5) are used as the basis for comparison. Although the addition of seasonal growth was significant for both the annual and biannual models, the greater improvement in log-likelihood generated for the annual models may be an artifact of the method of renumbering months to simulate biannual cohorts. This requires further investigation.

Table 5. Fits to albacore length-frequency data for MULTIFAN systematic searches that assumed biannual cohorts. These fits assume the same number of cohorts as the respective best-fitting annual models.

Parameter	Systematic search							
	B1	B2 SB	B3 ADSD	B4 SG	B5 SB ADSD	B6 SB SG	B7 ADSD SG	B8 SB ADSD SG
K (yr^{-1})	0.126	0.380	0.146	0.538	0.396	0.460	0.172	0.398
L_∞ (cm)	197.5	108.2	180.2	94.4	111.2	105.7	165.0	111.3
No. cohorts	5	7	5	9	6	7	5	6
First length (cm)	57.69	57.41	57.34	57.43	56.04	56.05	57.29	56.26
Last length (cm)	88.69	91.96	88.56	90.12	90.75	93.22	88.54	90.97
Age of 1st cohort (yr)	2.75	1.99	2.61	1.75	1.77	1.64	2.49	1.76
Sampling bias month 1 (cm)		0.000			1.368	1.615		1.101
Av. sd (cm)	2.296	2.150	2.417	2.048	2.364	2.210	2.415	2.359
First sd/ last sd			1.551		1.499		1.669	1.494
Seasonal growth								
Amplitude				0.114		0.357	0.314	0.370
Phase (mo)				-0.114		-0.239	-0.196	-0.238
No. Parameters	40	59	41	78	51	61	43	53
Log-likelihood	11742.1	11783.7	11817.7	11851.4	11820.4	11827.6	11853.0	11861.8

Consistency with tag-return data

It is possible to check the consistency of the best-fitting annual and biannual models with the limited tag-return data received to date. Four returns with recapture lengths are available. Details of the returns, along with the recapture lengths predicted by models A8 and B7, are presented in Table 6.

Table 6. South Pacific albacore tag-return data with recapture lengths predicted by models A8 and B7.

Release length	Days at liberty	Recapture length (cm)	Predicted recapture length (cm) Model A8	Model B7
72	868	88	87.5	104.2
78	404	86	84.9	93.7
80	494	92	87.4	95.4
76	199	80	79.9	84.4

The recapture lengths predicted by model A8 correspond closely to the actual recapture lengths in at least three of the four cases. On the other hand, model B7 overestimates the recovery length by amounts that vary according to time at liberty. Model A8 appears to be more consistent with these limited data.

Conclusions

1. The best fit to the length-frequency data was provided by an annual-cohort model incorporating sampling bias in the first cohort, age-dependent standard deviations in length-at-age and seasonal growth. For models in which seasonal growth was not included, the biannual-cohort models provided the better fit. This could be due to an artifact of the method used to introduce the assumption of biannual cohorts.

2. The best-fitting annual-cohort model is more consistent with available tag-return data, although more such data are required before this can be regarded as conclusive.

3. The question of annual or biannual cohorts therefore remains unresolved at this time. The explicit incorporation of biannual cohorts into the MULTIFAN model and more tagging data are required to further the analysis. Information regarding seasonality of spawning currently being collected will also be important in considering this question.

4. MULTIFAN shows considerable promise as a tool for length-based assessment of the South Pacific albacore resource. When all fishery data are assembled, the estimation of a time series of catch-at-age by gear type will be possible using the existing software. These estimates could then be input to standard age-structure stock assessment methods, e.g. cohort analysis. A preferable strategy would be to incorporate population dynamics sub-models into MULTIFAN for a completely integrated analysis. The integrated approach has the advantage of preserving the original error structure of the data, which results in more realistic estimates of confidence intervals about the parameter estimates of interest (e.g. optimum yield). The integrated approach can also better accommodate ancillary biological information that might be available, e.g. in the

form of tag-return data.

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Figure 1. Length-frequency samples with the best-fitting annual-cohort model indicated. The bars in samples 2 and 6 represent constraints placed on the mean lengths-at-age in those samples.

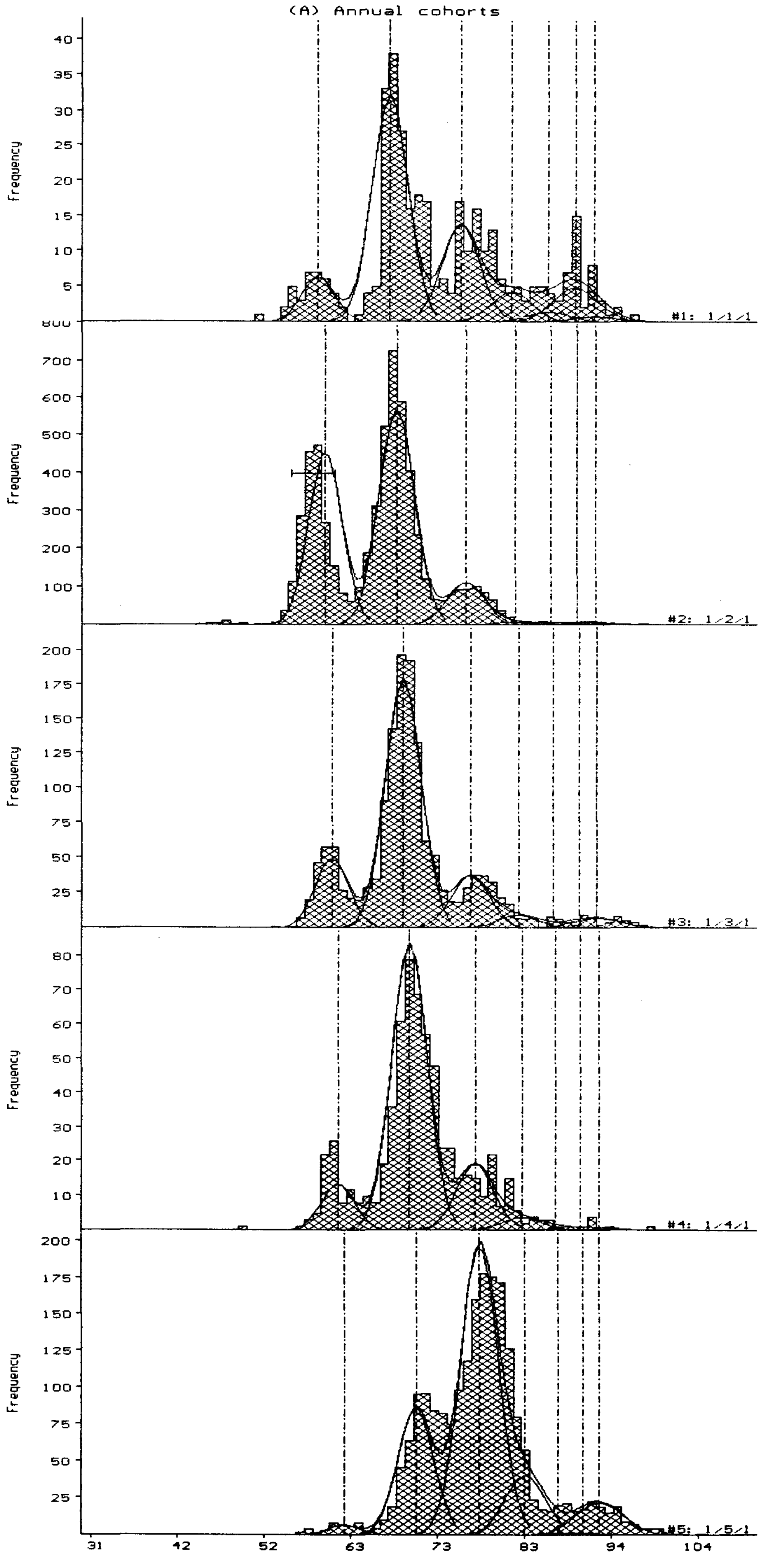
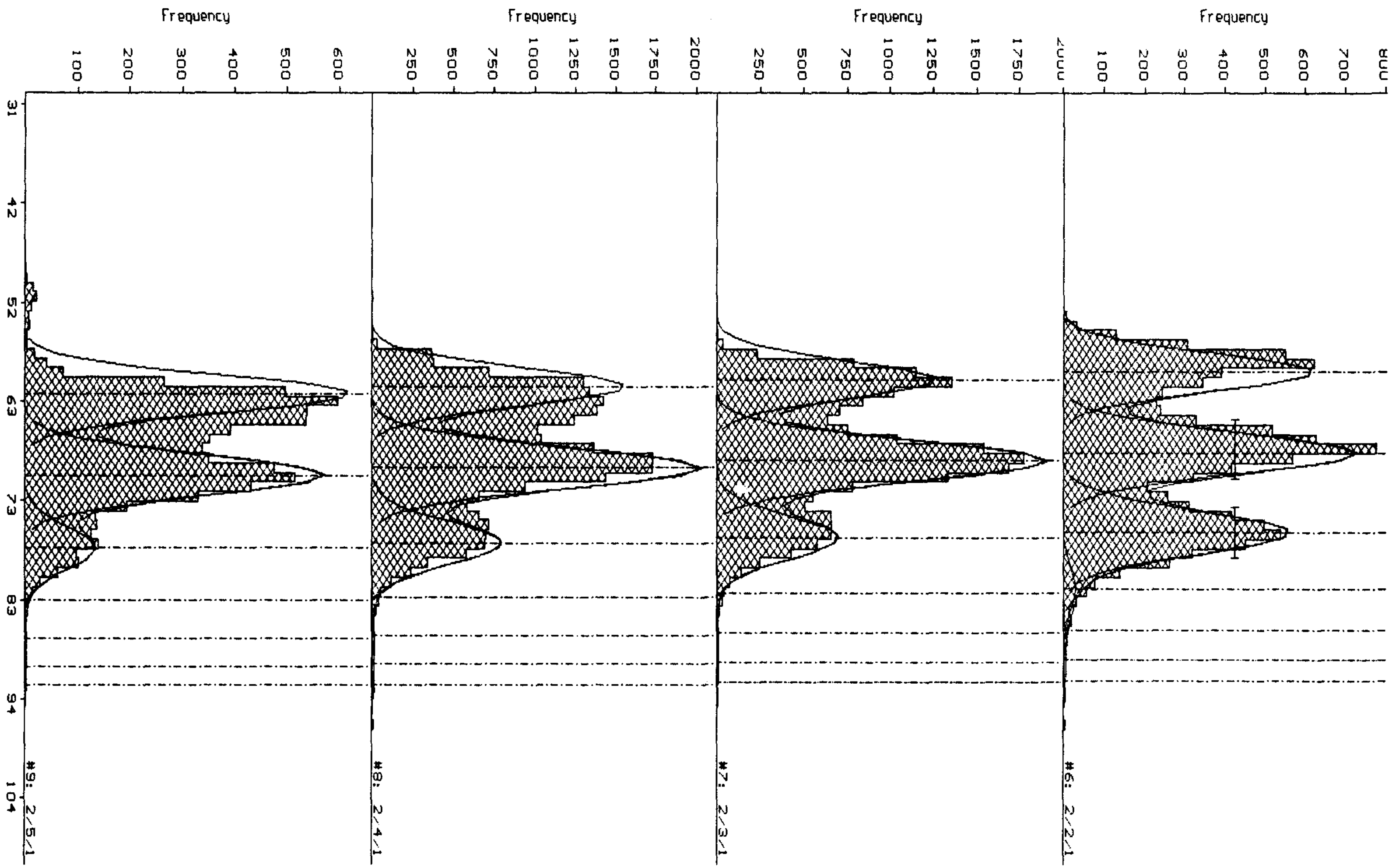

(A) Annual cohorts
Frequency
#1: 1/1/1
#2: 1/2/1
#3: 1/3/1
#4: 1/4/1
#5: 1/5/1
31
42
52
63
73
83
94
104

Figure 1 (continued)



Frequency
Frequency
Frequency
Frequency
#9: 2/5/1
#8: 2/4/1
#7: 2/3/1
#6: 2/2/1

Figure 2. Length-frequency samples with the best-fitting biannual-cohort model indicated. The bars in samples 2 and 6 represent constraints placed on the mean lengths-at-age in those samples.

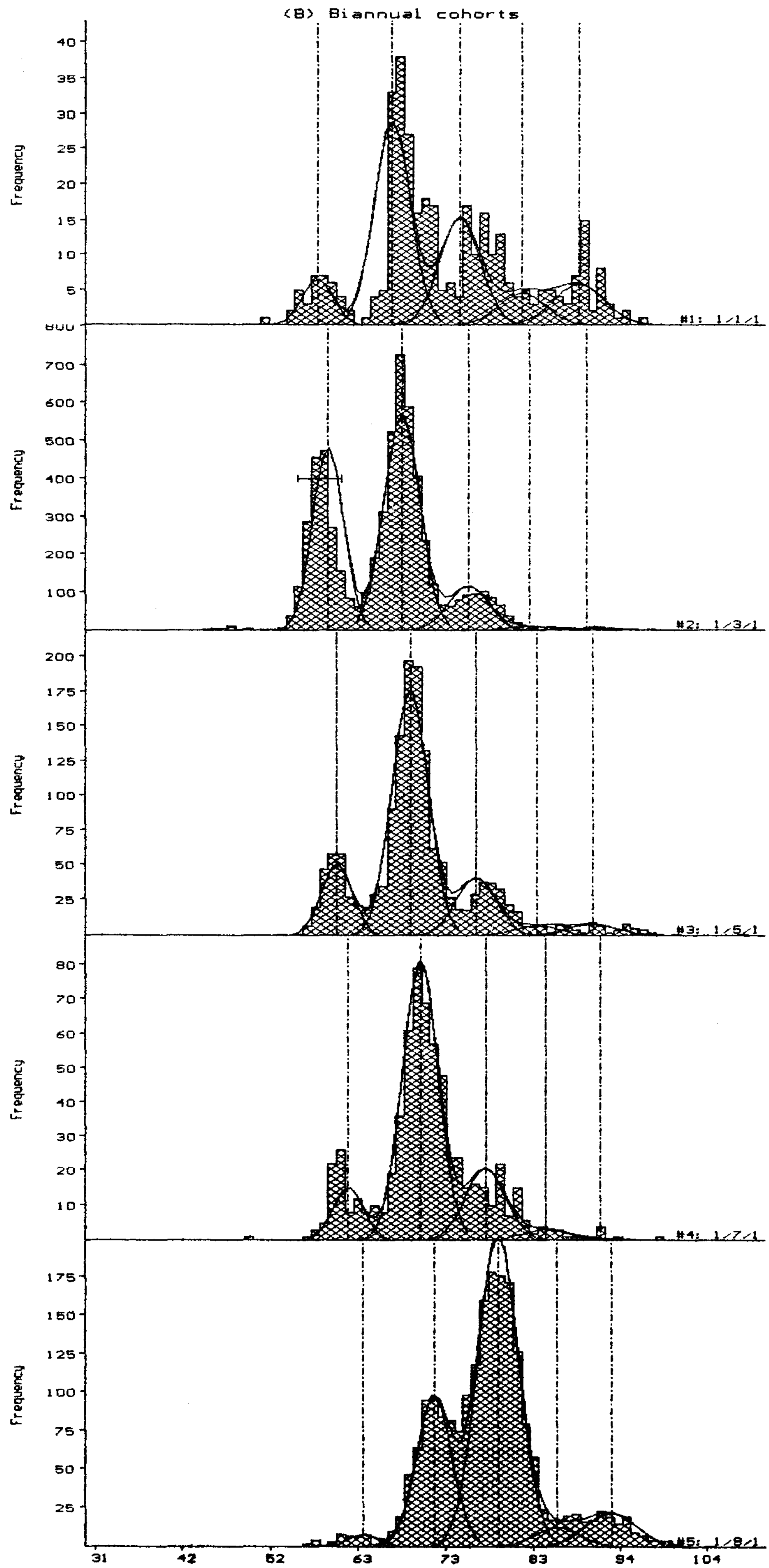
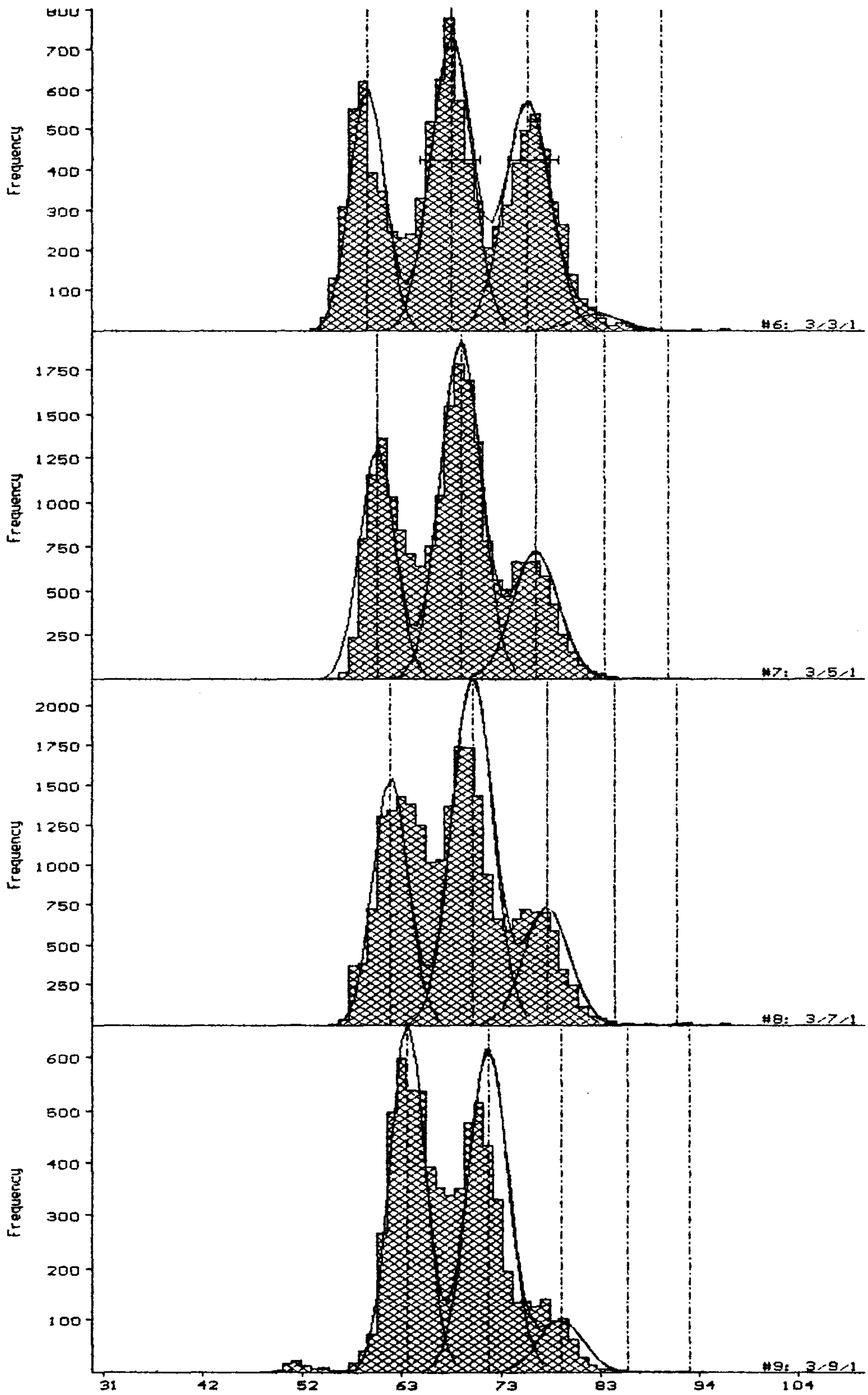
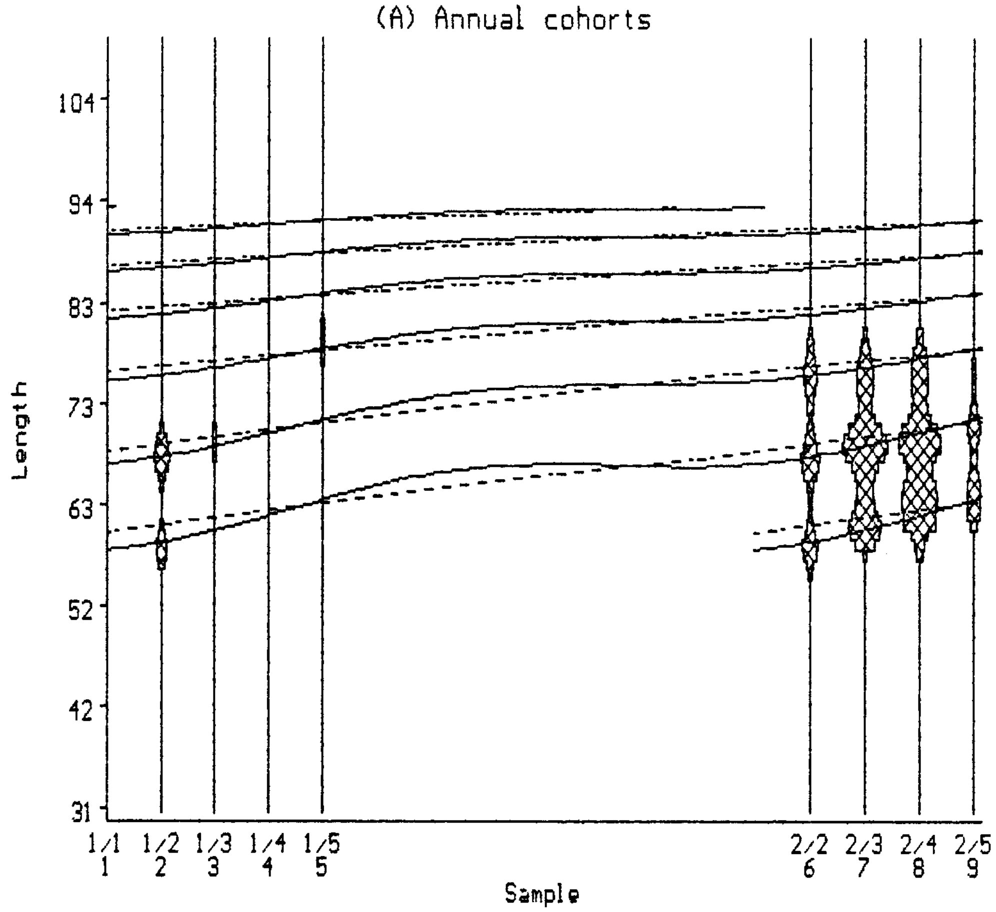

(B) Biannual cohorts
Frequency
#1: 1/1/1
#2: 1/3/1
#3: 1/5/1
#4: 1/7/1
#5: 1/8/1
31
42
52
63
73
83
94
104

Figure 2 (continued)



#6: 3/3/1
#7: 3/5/1
#8: 3/7/1
#9: 3/9/1
Frequency
31
42
52
63
73
83
94
104

Figure 3. Length-frequency samples and growth curves generated by the best-fitting annual-cohort and biannual-cohort models.



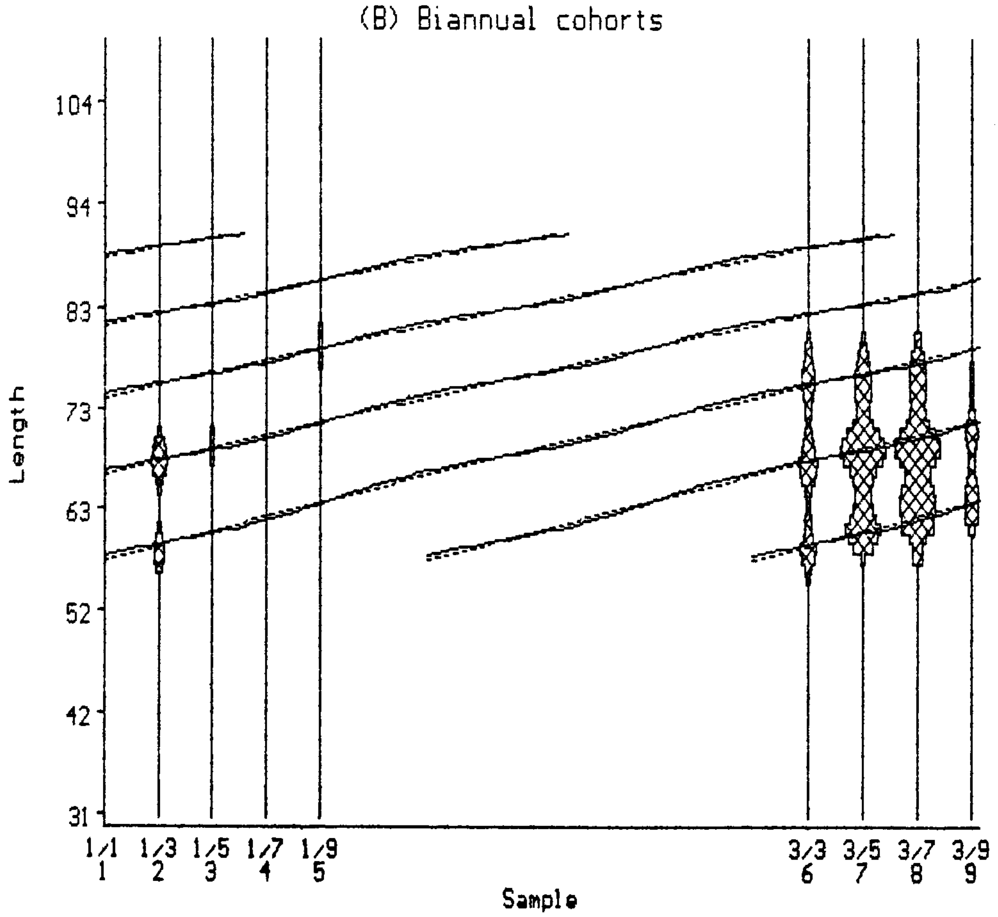


Figure 4. Growth curves generated by the best-fitting annual-cohort and biannual-cohort models.