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GROWTH RATES OF WHITE SHRIMP AS A FUNCTION
OF SHRIMP SIZE AND WATER TEMPERATURE

Scott Nichols

United States Department of Commerce
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Southeast Fisheries Center
Miami Laboratory
75 Virginia Beach Drive
Miami, Florida 33149

INTRODUCTION

Scientists studying the growth patterns of penaeid shrimp have never been really satisfied with "traditional" growth models used in fisheries research. The von Bertalanffy function is most frequently used, but with many sets of data, one finds that the relationship between length at some time (age) t and length at time $t+1$ is not really linear with time (age), and that the very existence of a meaningful asymptotic length is questionable. Other models with fixed parameters are used, but they too may show analogous indications of "lack of fit". Quite possibly, shrimp growth rates are too sensitive to environmental changes, particularly seasonal changes, to allow a good fit with any fixed parameter growth model, even if the basic model were correct under constant conditions.

Alternative approaches need to be explored, including incorporating temporal or spatial (or both) variations into single formulations. Phares (1980) has completed one analysis of seasonally-varying growth of white shrimp by expressing tail length as a function of degree days. Here, I will present another alternative, modeling growth rate directly as a function of shrimp size (tail length) and temperature, using data from mark-recapture experiments on white shrimp Penaeus setiferus L., in Louisiana, from 1977-1980.

DATA

White shrimp mark/recapture experiments have been conducted in both inshore and open Gulf waters by the NMFS's Galveston Laboratory and Louisiana Department of Wildlife and Fisheries since July 1977. A description of procedures can be found in Emiliani (1971) and Phares (1980). Data used in this paper include shrimp returned by 1 December, 1980. Records for which sex, tail length at release, tail length at recapture, and days at large data were incomplete were not included. Records for which the recorded recovery date preceded the release data were also rejected.

Water temperatures were recorded continuously at Caillou Lake, Louisiana, the primary inshore release site. Data were available from July 1977 to August 1979, with gaps from 8 August to 6 September, 1977; 21 November to 31 December, 1978; and 1 March to 1 April, 1979. For this work, the continuous data were summarized as average temperature for each calendar day. Gaps in the data were filled with the average of the last record before the first record after each gap, except for the November-December gap, which was filled with a linear drop in temperature between the available records.

To take advantage of additional releases beyond the existing temperature data, a cosine function was fit to the existing data (using BMDP3R; Dixon and Brown, 1979), and used to simulate temperatures for dates beyond the data. The cosine representation is not completely accurate (actual temperatures were slightly warmer in spring and fall, with a sharper minimum in the winter), but a cosine does serve as a reasonable approximation. Fig. 1 shows the inshore temperature data, and the simulated extension of those data.

No continuous offshore temperature data were available. I supplemented data taken on the offshore tagging cruises with monthly data reported by Lindner and Anderson (1956), and constructed a cosine function representing the annual cycle at about 10 fathoms depth (Fig. 2).

All shrimp released inshore were assumed to have lived in the environment described by the inshore temperature curve of Fig. 1. All shrimp released offshore were assumed to have lived under the temperature regime described by Fig. 2. Because individual shrimp may have moved anywhere in the spatial temperature gradient between release and recapture, the information lost by using simulated temperatures is probably small.

MODEL CONSTRUCTION

Growth rate at any instant, as the change in tail length per unit time, was assumed to be a function of tail length, temperature, and length x temperature interaction. The sexes were analyzed separately. Change in tail length (ΔL) divided by time at large (Δt) was used as an approximation of instantaneous growth rate. Length corresponding to each individual growth rate estimate was approximated by release length plus recapture length divided by 2. The corresponding temperature was approximated as the sum of the daily temperatures while at large, divided by the days at large. The effects of the length and temperature approximations are minor, although they do become more important with increasing time at large. The $\Delta L/\Delta t$ approximation presents some problems that must be expanded.

There are two major sources of difficulty in using $\Delta L/\Delta t$ as an estimate of instantaneous growth rate:

- 1) The errors in measuring tail length appeared to be large.
- 2) As the rates of 2 random variables, the distribution of $\Delta L/\Delta t$ will have "heavy tails".

In combination, these problems give $\Delta L/\Delta t$ a distribution with an unpleasantly large variance, and "too many" implausibly high (+ and -) observations.

The large number of tagged shrimp available for this study helps reduce the effects of these problems. However, for many needed combinations of length and temperature, the data are very sparse. Tables 1 and 2 show the numbers of observations available for different length and temperature ranges. Inclusion of implausible values in the sparse regions would result in a model that predicted impossible growth rates just outside the region of the data. Two actions were necessary to minimize this effect:

- 1) removing any implausibly extreme growth rate values
- 2) operating with mean growth rates over small ranges of length and temperature

The "heavy tails" caused by extreme $\Delta L/\Delta t$ values are reflected in the curvature of normal probability plots of the data (Figs. 3 and 4). Elimination of impossible rates was necessary, but any decision on the boundaries had to be subjective. I included all estimates between -0.5 and +1.5 mm per day, rejecting as too implausible the 10% of the observed rates (9% male, 11% female) outside that range. The distributions of the accepted data were nearly normal.

The relationship between growth rate and length and temperature was explored by plotting mean observed rates over 2° C and 5 mm length intervals ("cells" Figs. 5 and 6). Non-systematic variability was high, particularly for males, but in most cases the aberrant cells were those with low numbers of observations (see Tables 1 and 2). Two general points were suggested by Figs. 5 and 6:

- 1) The relationship between growth and length at a given temperature does not decline linearly with length, but passes through a maximum. The maximum growth rates occur at greater lengths with decreasing temperature (males and females both).
- 2) The relationship between growth and temperature, given length is described well for only a short span of lengths in these data. For males, growth rate increases with increasing temperature more slowly at higher temperatures and larger shrimp, but no maximum was apparent. The female pattern was similar, but larger females may have a maximum within or near the range of the data.

The simplest function that can capture the pattern suggested by the plots is:

$$G = b_0 + b_1L + b_2 L^2 + b_3T + b_4T^2 + b_5LT$$

with G the instantaneous growth rate; L , the length; T , the temperature; and the b 's as parameters. The coefficients of the model were estimated by linear

regression (using BMDP9R; Dixon and Brown 1979) performed on the cell means data, weighted by the number of observations in each cell. Tables 3 and 4 summarize the results of those regressions. One additional constraint was then added to the model: if predicted G is less than zero, predicted G is set = 0. Figures 7 and 8 map the predicted growth rates as a function of temperature and tail length.

White shrimp generally recruit to open inshore waters beginning at about 45 mm tail length, although some as small as 30 mm are encountered (data of Lindner and Anderson, 1956, Loesch 1965; total to tail length conversions of Brunenmeister, 1980). The distributions of the data points were shown in Tables 1 and 2, and the approximate limits are outlined in Figures 7 and 8. The predicted rates are probably valid down to recruitment in the open inshore waters at 45 mm. Predicted rates below 45 mm (outside the range of the data) are not consistent with observed rates for very small shrimp (see Lindner and Cook 1970), so I recommend against using the predicted rates below 45 mm.

The model predicts temperature-dependent maximum sizes for both males and females well outside the ranges of the data. The existence of such maxima is probably quite real, but because the predicted maximum values are so far removed from the data, the accuracy of the specific values is questionable. Setting a predicted upper limit to the predicted growth rates, analogous to the 45 mm lower limit, will really depend on the specific application intended.

Figures 9 and 10 show length vs time curves for a hypothetical sequence of cohorts recruited at 45 mm tail length from late June to November (2 weeks apart). To produce these curves, each cohort was assumed to exist in the temperature regime described by the inshore cosine curve fit to the Caillou Lake data (Figure 1) until early October. After that, once the predicted tail length for a cohort exceeded 54 mm, the temperature regime was assumed to follow the offshore curve (Figure 2). This approximates the fall emigration of shrimp at the sizes described by Pullen and Trent (1969) for Galveston Bay.

DISCUSSION

The apparent existence of a maximum in the relationship between growth rate and shrimp length was unexpected. Traditionally a linear (or at least monotonic) decline in growth rate with increasing length is hypothesized. At first, I doubted the reality of the maximum suspecting that the smaller shrimp may have been "too small" to tolerate the tag. However, the shift of the maximum to larger sizes at lower temperatures would be unlikely if interference from the tag were the main cause of reduced growth rates at smaller sizes.

The model predicts that shrimp recruited in June and July will reach about 140 mm tail length the following summer. Such sizes are uncommon. Either mortality is so great that most of the early cohorts are essentially eliminated in less than one year, or the sizes predicted by the model overestimate the true sizes, or both.

Cohorts recruited in June, July, and early August will grow "down the ridge" of high growth rates in Figures 7 and 8 throughout the summer, fall, and winter. Not until the following spring does growth rate show a sharp decline. (Dr. Susan Brunenmeister has pointed out that this predicted spring decline coincides with the onset of reproductive activity). The high rates predicted for midsummer cohorts are in contrast with the low rates predicted for fall recruits. The model predicts that shrimp recruited in November will remain inshore, and show essentially no growth until the following spring. The model's structure for handling emigration to offshore waters is crude, but the pattern is in accord with length-frequency observations of Lindner and Anderson (1956) and Loesch (1965), which show essentially static modal sizes inshore during the winter.

Variation between the predicted rates and observed cell means was large (note the R^2 in Tables 3 and 4), but systematic variation was not obvious. However, many of the sparser cells were filled by data from single release groups. Clearly, temperature and size do not completely determine growth rates, but I believe that much of the truly seasonal component of variation has been captured in the model. The limitation is that other, non-seasonal components exist with magnitudes of importance roughly on a par with seasonal variation.

CONCLUSIONS

The mechanistic nature of this growth model is its most appealing feature. Allowing growth rate to respond directly to other variables appears to be both realistic and powerful. Only temperature and size were considered here, but other variables could be included if desired. The model is completely general, in that no specific size-at-age function is required, although it is capable of creating curves of specific functions if the data warrant.

The major difficulty with this approach is that the data available were "ill-conditioned" for obtaining parameter estimates. This problem will probably exist for any field-oriented growth experiments. Data were sparse for many combinations of the independent variables. This exacerbated the difficulties caused by using $\Delta L/\Delta t$ as an approximation to instantaneous growth rate. Subjective decisions about the data had to be introduced. Residual variation remained large, in part because individual growth variations were probably large, in part because measurement errors were large, and became magnified using a $\Delta L/\Delta t$ approach.

Problems in applications of the model for white shrimp stem primarily from extrapolation beyond the range of the data, which unfortunately, is usually required. I remain suspicious of the predicted growth rates above about 90 mm

tail length, and of the size-at-time curves at those sizes. The seriousness of the problem depends on the application. The problem should be minimal when using this model in yield in weight functions associated with yield per recruit models.

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TABLE 1. Number of Observations in 5 mm By 2°C Cells. Males

	Tail Length (mm)														
	<45	45-50	50-55	55-60	60-65	65-70	70-75	75-80	80-85	85-90	90-95	95-100	100-105	105-110	>110
≥30	1	23	70	159	166	181	160	105	44	7	1	2			
28-30	17	36	37	36	31	48	42	25	18	6	2				
26-28	1	4	12	19	23	42	50	26	18	10					
24-26	1	1	2	7	19	51	108	105	71	40	16	6	1		1
22-24		2	17	22	44	83	54	29	7	6	4	6	5		1
20-22		1	4	2	3	6	2	1	1		2				
18-20	1	1	2		2	2	13	24	34	26	20	11	3		
<18			2			6	8	28	30	15	11	7	3		1

TABLE 2. Number of Observations in 5mm by 2°C Cells. Females

	Tail Length (mm)														
	≤45	45-50	50-55	55-60	60-65	65-70	70-75	75-80	80-85	85-90	90-95	95-100	100-105	105-110	>110
≥30	3	31	87	175	171	173	159	119	61	21	16	1			
28-30	11	49	55	63	48	79	73	37	29	14	6	3			
26-28	2	16	23	23	38	48	47	45	20	10	5	3			
24-26		1	7	18	13	50	92	114	96	74	22	11	1	3	2
22-24	7	25	34	60	71	93	71	35	17	11	3	3	1		1
20-22		3	4	22	6	7	5	3		1			1		1
18-20	1	2	1	2	4	4	15	32	40	29	22	10	18	7	3
<18		1		2		3	16	33	33	24	11	14	7	3	4

Table 3. Summary of regression statistics, males. Output from BMDP9R, Dixon and Brown (1979).

SQUARED MULTIPLE CORRELATION 0.58128
 MULTIPLE CORRELATION 0.76242
 ADJUSTED SQUARED MULT. CORR. 0.54579
 RESIDUAL MEAN SQUARE 0.006664
 STANDARD ERROR OF EST. 0.081634
 F-STATISTIC 16.38
 NUMERATOR DEGREES OF FREEDOM 5
 DENOMINATOR DEGREES OF FREEDOM 59
 SIGNIFICANCE 0.

VARIABLE NO.	NAME	REGRESSION COEFFICIENT	STANDARD ERROR	STANDARD COEFF.	T-STAT.	2TAIL SIG.	TOLERANCE	CONTRIBUTION TO R-SQUARED
	INTERCEPT	-2.24324	1.20115	-18.519	-1.87	0.067		
2	L	0.0303993	0.0169398	2.037	1.74	0.078	0.002834	0.022855
3	T	0.0863683	0.0547081	2.921	1.58	0.120	0.002074	0.017688
5	LSQ	-0.0000932129	0.0000737514	-1.241	-1.26	0.211	0.007360	0.011337
6	TSQ	-0.000383294	0.000744518	-0.856	-0.51	0.609	0.004369	0.001881
7	LXT	-0.000587585	0.000324036	-1.556	-1.81	0.075	0.009634	0.023336

Table 4. Summary of regression statistics, females. Output from BMDP9R, Dixon and Brown (1979).

SQUARED MULTIPLE CORRELATION 0.54410
 MULTIPLE CORRELATION 0.77052
 ADJUSTED SQUARED MULT. CORR. 0.56528
 RESIDUAL MEAN SQUARE 0.005899
 STANDARD ERROR OF EST. 0.076803
 F-STATISTIC 20.79
 NUMERATOR DEGREES OF FREEDOM 5
 DENOMINATOR DEGREES OF FREEDOM 71
 SIGNIFICANCE 0.

VARIABLE NO.	NAME	REGRESSION COEFFICIENT	STANDARD ERROR	STAND. COEF.	T-STAT.	2-TAIL SIG.	TOLERANCE	CONTRIBUTION TO R-SQUARED
	INTERCEPT	-3.18010	0.826757	-27.291	-3.85	0.000	0.003987	0.063268
2	L	0.0367000	0.0110311	3.284	3.33	0.001	0.002622	0.067472
3	T	0.143113	0.0415548	5.072	3.44	0.001	0.009543	0.027940
5	LSQ	-0.000107964	0.0000488329	-1.711	-2.21	0.030	0.004623	0.027024
6	TSQ	-0.00135301	0.000622250	-2.18	-2.17	0.033	0.012870	0.063803
7	LXT	-0.000723210	0.000216467	-2.226	-3.34	0.001		

Figure 1. Inshore temperature vs time. Data from Caillou Lake, Louisiana. The smooth curve after August, 1979 is a cosine curve fit to the 1977-1979 data.

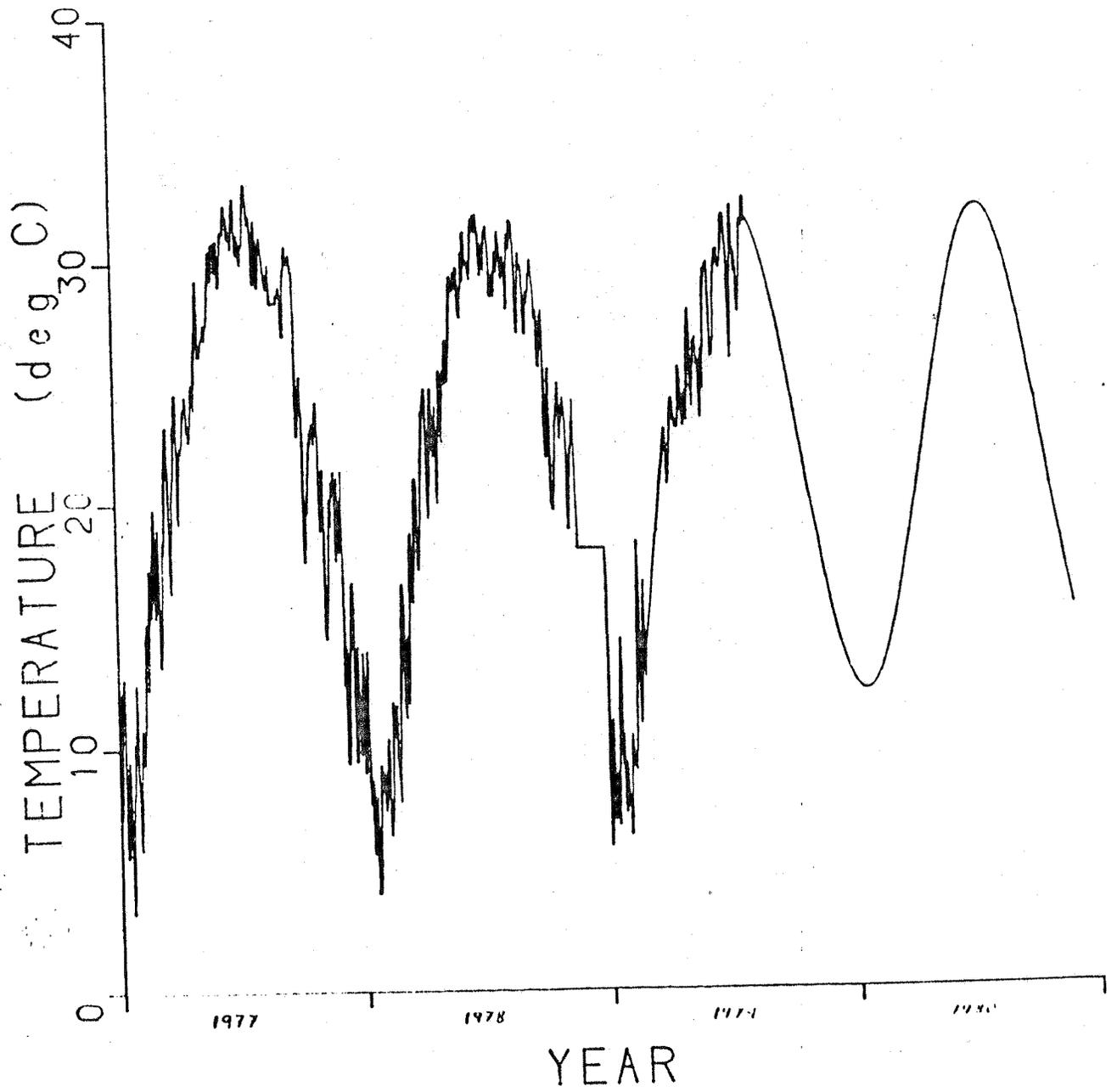
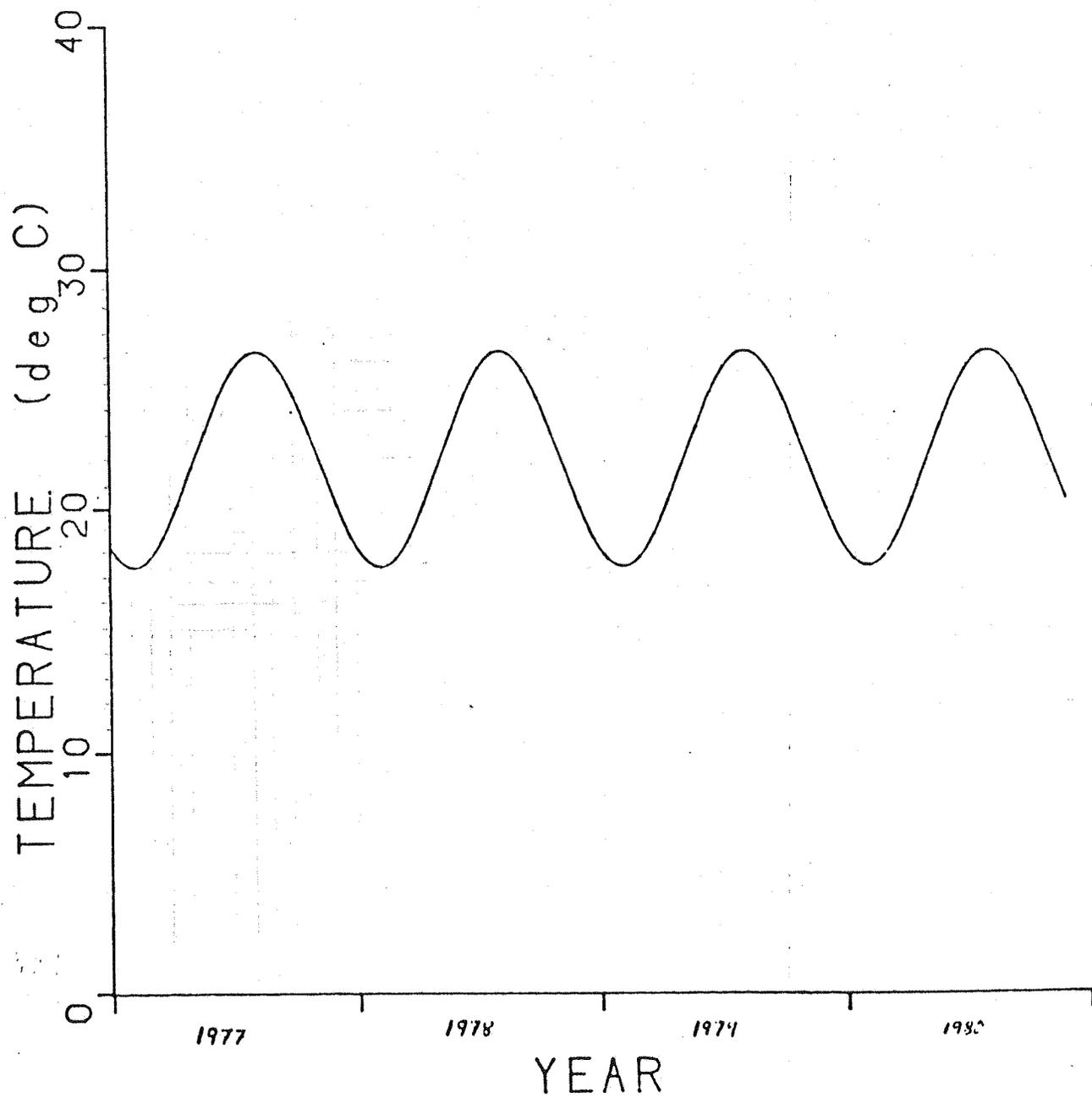


Figure 2. Simulated offshore bottom temperature vs time.



The figure is a copy of output from BMDP5D (DIXON and BROWN 1979).

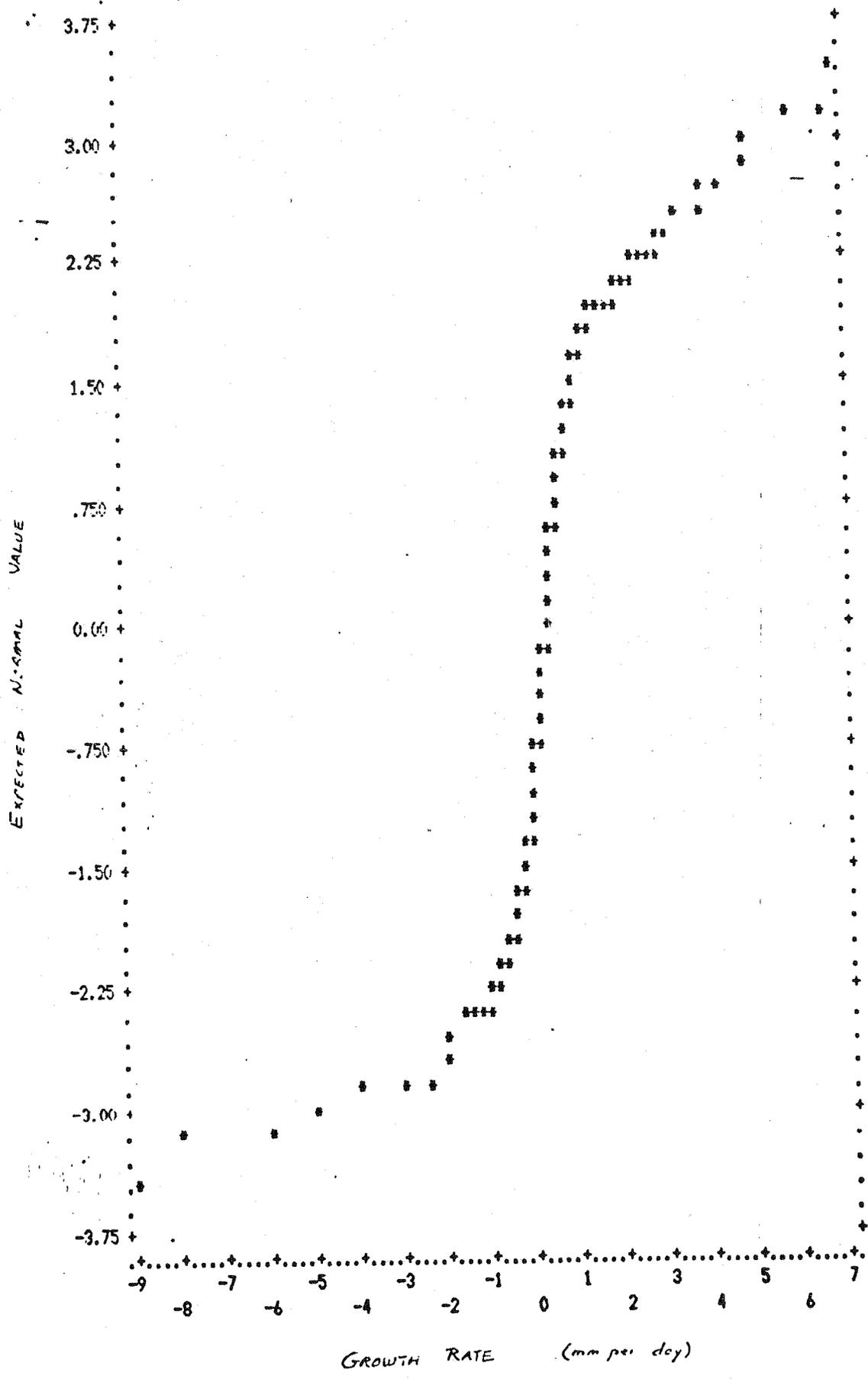


Figure 4. Normal probability plot for observed growth rates of females. This figure is a copy of output from BMDP5D (Dixon and Brown 1979)

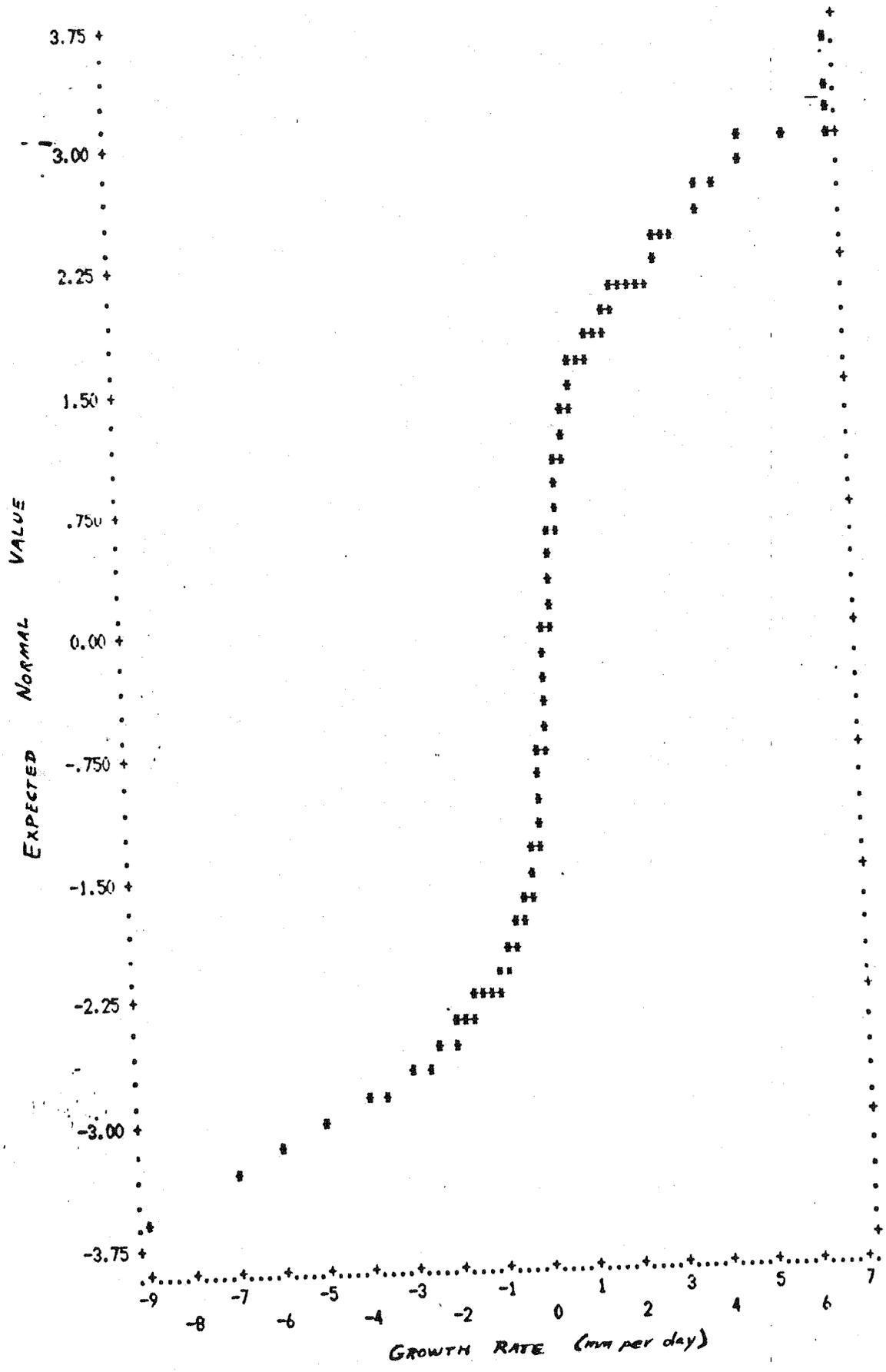


Figure 5a. Observed mean growth rates vs. tail length, male.

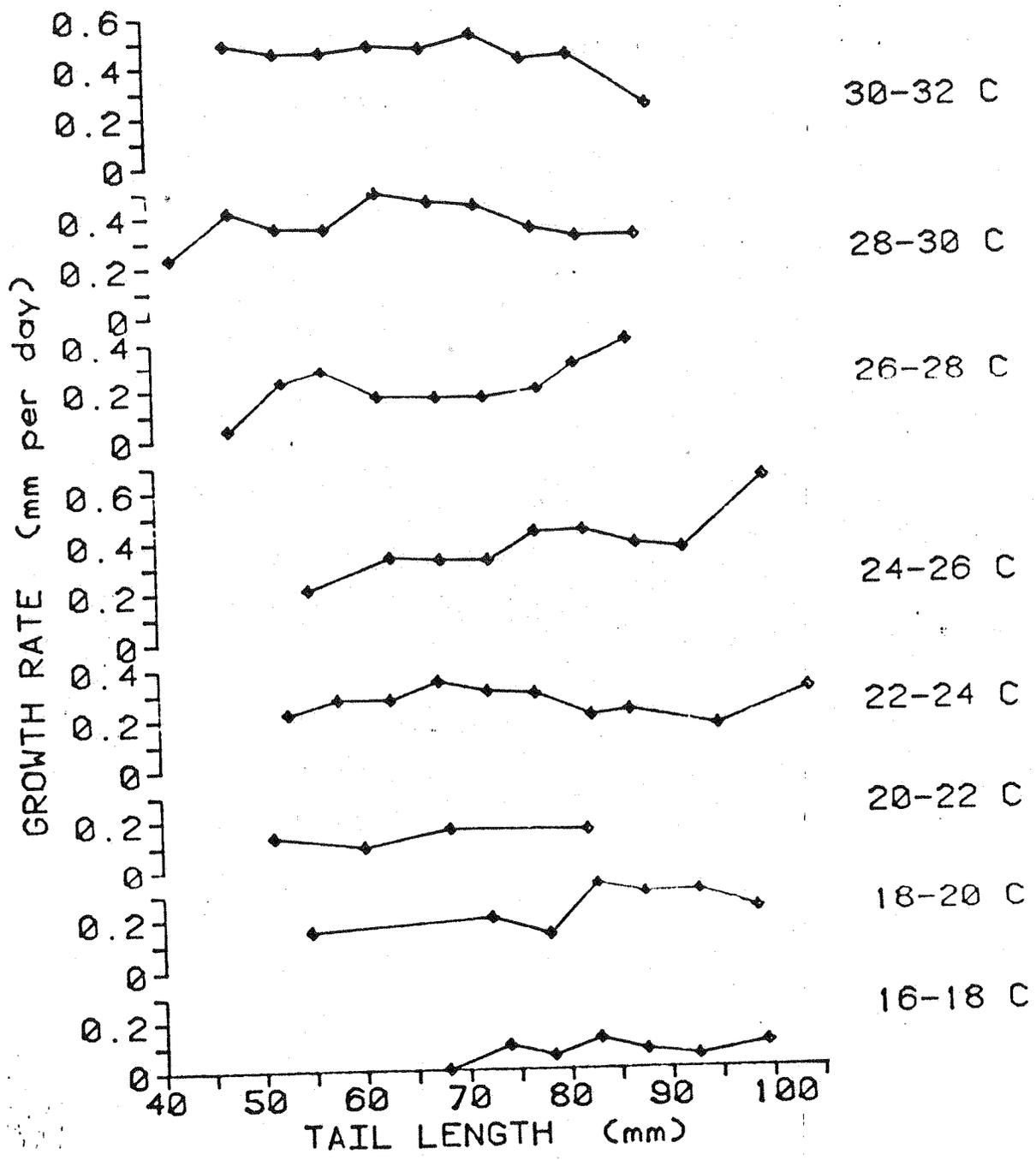


Figure 5b. Observed mean growth rate vs temperature, males (To reduce the number of curves presented, this figure is plotted with 10 mm length groupings. The original "cell" summaries used 5 mm groupings).

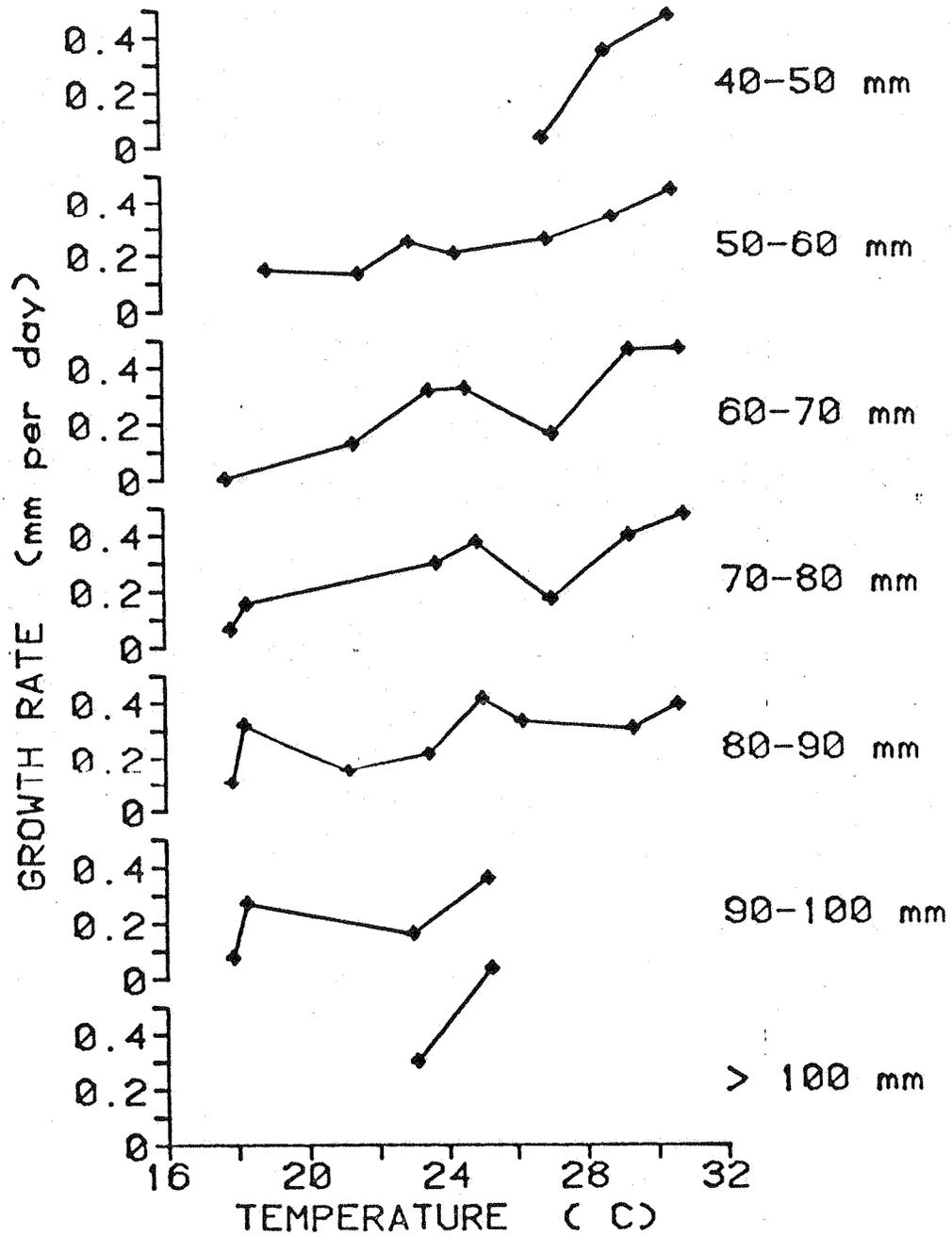


Figure 6a. Observed mean growth rates vs tail length, females.

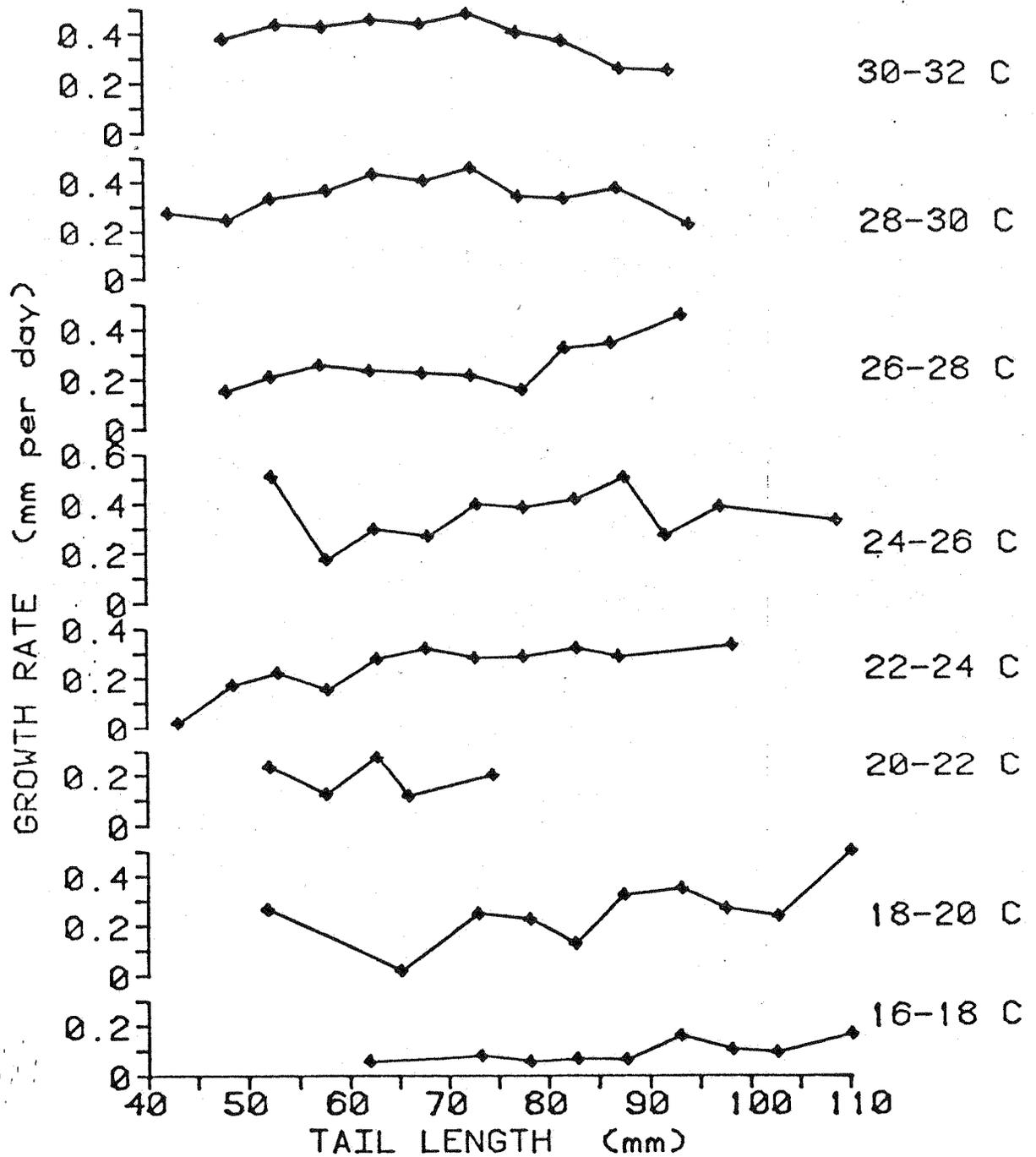


Figure 6b. Observed mean growth rates vs temperature, females.
 (To reduce the number of curves presented, this figure
 is plotted with 10 mm length groupings. The original
 "cell" summaries used 5 mm groupings).

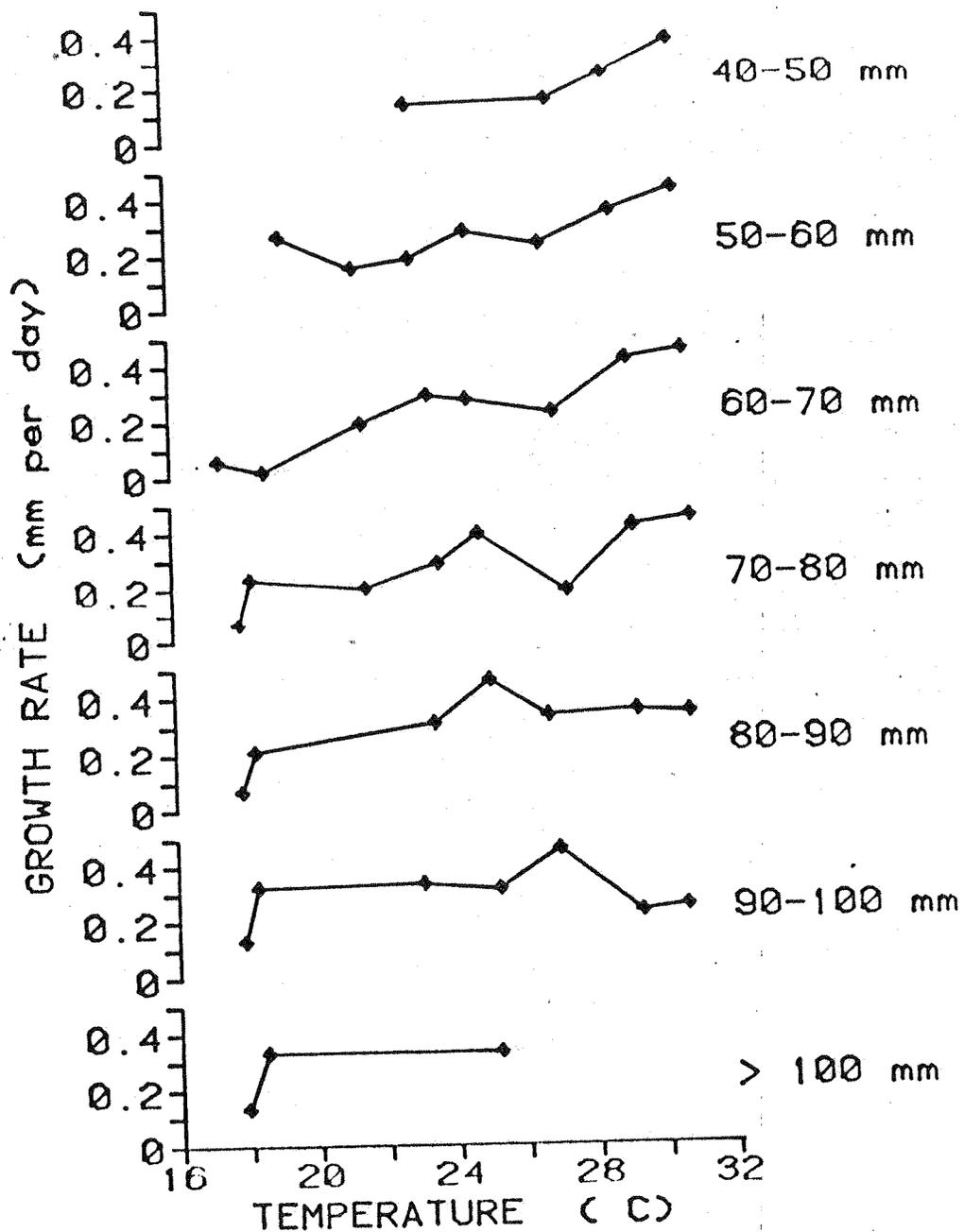


Figure 7. Predicted growth rates vs temperature and tail length, males. Growth rate contours are in mm per day.

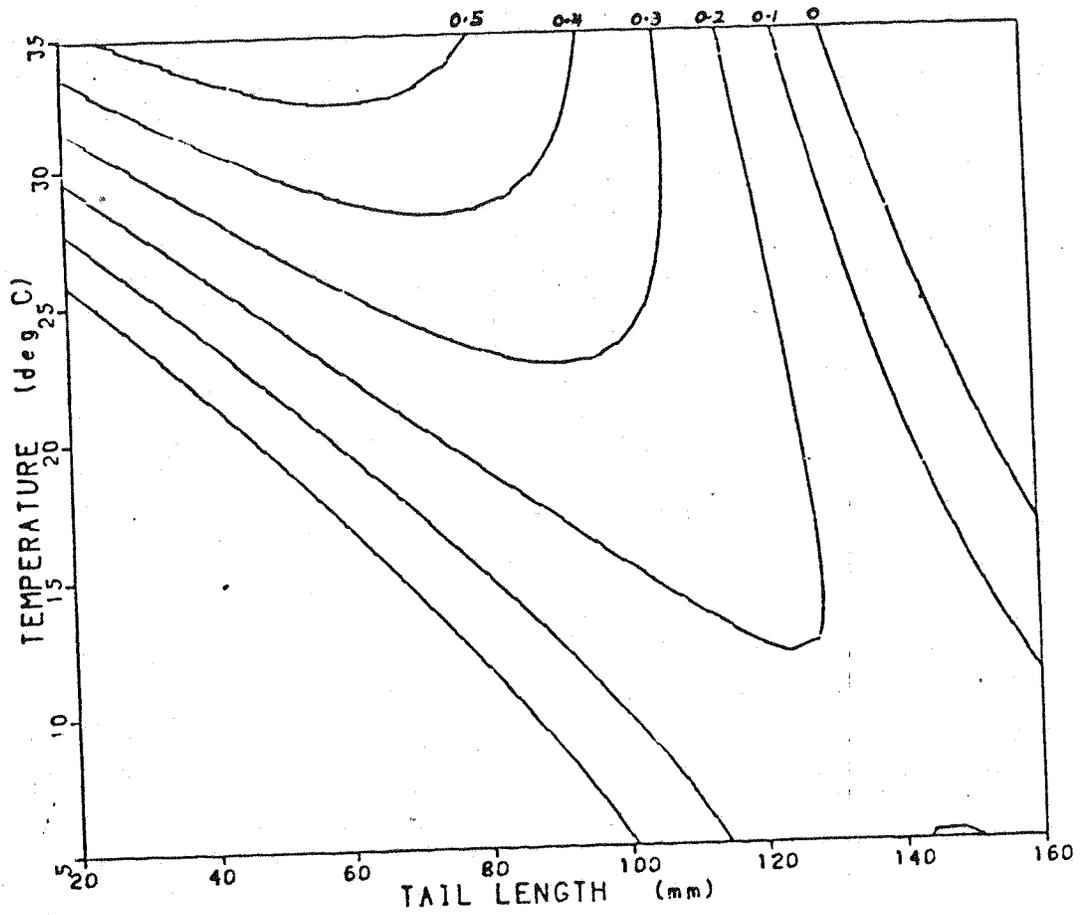


Figure 8. Predicted growth rates vs temperature and tail length, females. Growth rate contours are in mm per day.

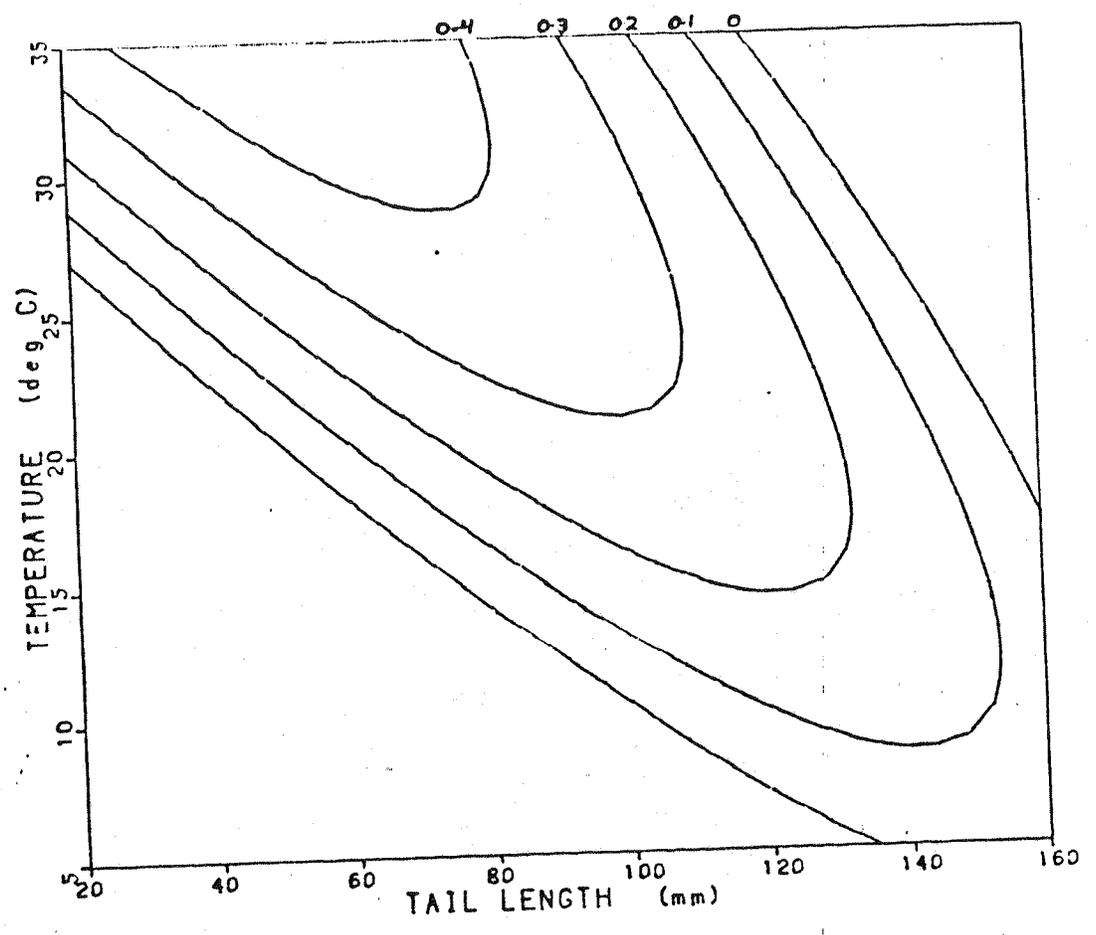


Figure 9. Tail length at time for a sequence of cohorts, males. The cohorts "recruit" at 45 mm tail length at 2 week intervals.

