

INTERNAL REPORT 147

BENTHIC MACROINVERTEBRATE PRODUCTION

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ABSTRACT

Macroinvertebrates were sampled on a regular basis from March to October 1973. A relationship between chironomid length and biomass was established. Production equations to be used for these insects are reported. A similar length/weight relationship is presently being explored for the oligochaetes. A proposal is made for calculating their production as well as for sphaeriids and *P. affinis*. Sampling is expected to continue at least through March 1974 to give a full year's data. In the near future the results of this study are to be correlated with studies concerning primary production, fish feeding habits, lake sedimentation rates, and physical properties.

INTRODUCTION

The study reported here is to estimate benthic macroinvertebrate biomass and productivity in the four IBP lakes for the purpose of comparison. In addition, this information will serve as input to a model on overall lake productivity and will relate detrital input to the food web. The question of whether or not the detrital food chain contributes significantly to fish production is of interest and will be pursued.

Monakov (1972), Sorokin and Meshkov (1957), Brinkhurst and Chau (1969), Johnson and Brinkhurst (1971a, b, c), Lellak (1965), and Izvekova (1969) show that the majority of macrofaunal feeding in the lake sediments is detrital and that sedimentation rate and benthic productivity are directly related. Hence, in this investigation the benthic macrofauna are assumed to be detrital feeders. However, it is recognized that in the more littoral regions carnivorous behavior is prominent. Due to the depth and bottom characteristics of the lakes, benthic algal production is minimal, leaving bacterial and invertebrate contributions to productivity the only significant ones.

Patriarche and Ball (1949), Hayne and Ball (1956), and Fred Olney (1972) show that benthic fish feeding on invertebrates is selective. Dipterans seem to be the food of choice even when they don't represent the bulk of benthic biomass. Therefore, greater attention is given to these insects and their productivity is calculated separately.

METHODS

Macrobenthos populations were sampled from March to October 1973 on a regular basis. Dates and sites sampled are shown in Table 1 and Figure 1. Bottom types at these stations are given in Table 2. The samples were taken either with a Van Veen or an Ekman dredge and screened with a 0.5-mm-opening-size mesh. The organisms were manually separated from the detritus and stored in alcohol. Detrital particles of a size greater than 4 mm were retained, separated as to their refractile or nonrefractile nature and weighed after air drying. From two to four samples per station were taken depending on the size of the sampler. For more information concerning the analysis of these samples, please see Table 1.

LIFE HISTORY OF THE CHIRONOMID LARVAE

There are usually four instars for chironomids. Jonasson (1965) shows the relative sizes of *C. anthracinus* Zett. (Figure 2). The instar analysis for all the chironomids for Sammamish station 1 and Findley station 1 are shown in Figures 3 and 4 respectively. In agreement with Jonasson (1965), Oliver (1971), Miller (1941), and Lellak (1965), chironomid growth occurs mainly in spring and fall. There are several reasons for this. We have assumed the chironomids are detrital feeders. Detritus in the lakes is comprised of autochthonous (e.g. dead algae and zooplankton) and allochthonous (e.g. leaves, conifer needles, wood chips) material. The supply of these to the bottom is not constant over the year. In large lakes, Lellak (1965) and Jonasson (1965) have shown that the autochthonous material contributes the majority of the detritus while in small lakes, ponds, and streams allochthonous is most significant (Nelson and Scott 1962, Chapman 1963, Teal 1957). Lake Washington, Lake Sammamish, and probably Chester Morse of our system fall into the first category while Findley possibly falls in the second. Primary productivity, sedimentation, and allochthonous input data will indicate whether this hypothesis is true. If correct then we would expect to see a rise in chironomid production in spring, remaining elevated over the summer, with a decline towards winter. Figures 3 and 4 show a rise in spring but a stagnation in the summer and, in the first case, a burst of growth before winter. This can be explained by inspection of the benthic environment over the summer period. Sammamish goes anaerobic over the summer. It is known (Berg, Jonasson, and Ockelmann 1962, Berg and Jonasson 1965) that chironomids can live for long periods at very low concentrations of oxygen. However, at these low concentrations little if any growth occurs. In fact, Jonasson (1965) recorded an actual weight loss during this period. Lack of oxygen and possibly low temperatures severely restrict larval metabolism. However, due to the small range of temperature changes in the bottom in large lakes over the year, temperature may be insignificant as a metabolic regulator.

In the fall the thermocline begins to break down and in Findley overturn occurs around October. Oxygen and a slight rise in temperature allow metabolic activity to increase. Stagnation over the winter occurs from lack of food and again a weight loss may occur (Jonasson 1965).

It would be extremely interesting to correlate the production of chironomids with temperature data from the water column and the bottom, oxygen concentration on the bottom, primary production, allochthonous input, and sedimentation data to find what the controlling factors are. This is proposed for 1974.

No classification of the larvae has yet been attempted. Chironomid taxonomy is extremely difficult and usually must be done by experts in the field. Therefore, arrangements have been made with a chironomid taxonomist to classify the ecologically important species. In this way more precise life history information can be used to compute production.

DATA ANALYSIS

Biomass

Wet weight, dry weight, and length data have been compiled on chironomid larvae and a nonlinear regression has been run on the three parameters. The length of the organism is the independent variable and wet weight and dry weight are dependent variables. The resulting graphs are shown in Figures 5-12 for Findley and Sammamish.

The equation chosen to represent the relationship is:

$$wt = aL^b \quad (1)$$

where wt is the weight of the organism, L is the length, a can be thought of as a density parameter, and b represents the manner of growth.

If the radius r of an organism is constant as growth occurs then it is growing in essentially one direction and

$$wt = aL \quad (2)$$

where $a = \pi r^2$. If r increases proportionally to L ($r = xL$) then:

$$wt = \pi(r^2)L = (x^2L^2)L = \pi x^2L^3 = aL^3. \quad (3)$$

It was expected that b would be close to 3 for our organisms. To find b a two-parameter model was used allowing both a and b to vary. Figure 5 shows the results of this two-parameter model for Findley. As expected, b was very close to 3 (3.1666) giving the equation:

$$wt = 2.47431 \times 10^{-6}L^{3.1666} \quad (4)$$

In this case length explained 87.8171% of the variation in wet weight. Figure 6 shows a one parameter model with the constraint, $b = 3$. The resulting equation is:

$$wt = 3.93554 \times 10^{-6}L^3. \quad (5)$$

In this case length explained 87.7170% of the variation in wet weight. The second parameter explained only about 0.1% and so can be dropped.

The dry weight data was much more difficult to obtain and is not so precise. Problems were encountered with moisture absorption in the time it took for the balance to stabilize while weighting. Consequently, using the two-parameter model, b was not as close to 3 as we would like to see (Table 3). However, knowing that b must be close to 3, it was constrained at 3 using the one-parameter model and 82.3711% of the variation in dry weight was explained. Subtracting the sum of squares of the two-parameter model from the sum of squares of the one-parameter model, it was decided that the difference could be explained by four points being off by 10%. The total accuracy of the weighings is not good enough to ascertain this.

Similar data has been obtained on Lake Sammamish, Lake Washington, and to a lesser extent on Chester Morse. This enables measurement of the length parameter to obtain the biomass.

PRODUCTION

Many ways are available to compute production (Hynes & Coleman 1963, Hamilton 1969, Fager 1969, Ness and Dugdale 1959, Teal 1957, Odum 1957, Mathias 1971, Waters 1969, Johnson and Brinkhurst 1971, Edmondson and Winberg 1971). Initially, yearly production for chironomids will be computed from biomass data. Monthly production for these larvae is not a very meaningful calculation due to their growth characteristics as shown above. Yearly production can be calculated using equation (6). However, it is easier to compute the production for a generation and then adjust to the time per generation. Equation (7) calculates production per generation assuming that the biomass at the start is zero.

$$\text{Production} = \text{g/yr Emergence} + \text{g/yr Mortality} + \Delta \text{ in standing biomass.} \quad (6)$$

$$\text{Production} = \frac{\text{Emergent Biomass } (B_E)}{T_E} + \frac{\bar{B}(\% \text{Mortality})}{T_E} \quad (7)$$

where T_E is the time from the start till they emerge. Emergence as used here refers to emergence from the mud as pupae, not emergence from the lake. The number of emergences per year can be obtained from our taxonomic data combined with what we know about the environmental conditions. Having obtained this, mortality rates can be calculated from our data (equations 3-10) by plotting numbers per square meter per generation at a single depth. Jonasson (1965) has done this and found low predation during most of the year except from autumn overturn until decreases in temperature are such that they cause the activity of poikilothermic animals to drop. In contrast pupal mortality is extremely high. Correlation with fish stomach analysis is slated for 1974. The mortality rate obtained times the average biomass will give the amount of production lost per generation due to natural causes.

$$B_t = B_o e^{-Mt} \quad (8)$$

$$\frac{dB}{dt} = -MB_o \quad (9)$$

$$B_0 - B_t = B_0 (1 - e^{-Mt}) \quad (10)$$

To divide the production figure by the number of months per generation would give an erroneous picture of the growth pattern. However, seasonal growth rates will be obtained from data such as appear in Figures 3 and 4. Continued sampling until March 1974 will generate enough data to complete production calculation.

OLIGOCHAETES

It is difficult to deal with this group of invertebrates. Their taxonomy is about as complex as chironomid classification and their life histories are less well known. They are detrital feeders and behave similarly to their relatives, the annelids, on land. Population parameters are difficult to obtain due to their mode of growth. Length cannot be used as a measure of growth because quite often they are broken apart during the sampling operation. Also preservatives cause them to contract to varying degrees so the natural length is obscured. Growth does not take place in instars as for the insects.

Presently, the possibility of a length/weight relationship is being explored. Under the circumstances, such a relationship would be expected if growth occurred mainly in one direction, i.e. increases in length occurred much faster than increases in diameter. Then, even if the organisms were broken up, biomass could be calculated from length data--a much simpler method than weighing individual animals. Since we are only looking for a predictive tool concerning the computation of the average biomass, the preservative problem should not enter in. This work is in its final stages of completion and will soon show whether this hypothesis is correct. If true, the biomass data will be relatively easy to obtain and could be completed within a few months.

Production estimates cannot be obtained directly from the data as in the case of the chironomids. Literature values for turnover ratios such as reported by Johnson and Brinkhurst (1971) will have to be used. Figure 13 shows the relationship between mean annual temperature and the turnover ratio. While annual turnover ratios may vary, the observation has been made by several authors that life-cycle turnover ratios remain remarkably constant for many invertebrates (Table 4). Such values can be used to approximate production figures if the life-cycles of the oligochaetes are known.

Preliminary examination of the worms shows that the majority are tubificids. Further classification will be done by an oligochaete taxonomist. Knowledge of the mean annual temperature and the major species of tubificids will indicate the lifecycle.

SPHAERIDS

The Sphaeriidae occur at some stations in great numbers (Table 1). These are usually littoral to sublittoral stations relatively free of fine mud. Stable sand and gravel with low turbidity is the normal habitat. Comparing the bottom types with stations populated with sphaerids bears this out.

Surprisingly, sphaerids are common in lakes which have a pH as low as 6.0 and CO₂ concentrations of only 2.0 mg/l (Pennak 1953). Yet, their CaCO₃ shells can be maintained. Sphaerids have adapted to a wide range of habitats and conditions.

Sphaerids are hermaphroditic and the young mature almost completely inside the parent. They are released, shell and all, when they reach about 1/4-1/3 the size of the adult. Reproduction can occur throughout the year but is low in the winter. Severe winter conditions (e.g. low temperatures, ice) are withstood by burrowing deeper into the bottom. Sphaerids are thought to live about 12-18 mo (Pennak 1953).

The production estimates can be approached by two methods. Using the turnover ratios already mentioned, production would be relatively easy to calculate. A more accurate but much more time-consuming method would be to calculate growth rates by microscopic examination of the rings on the shells. However, due to the difficulty of this method and the shortness of the life span the former method will be used.

Biomass data will be determined by weighing the animals in the shell, allowing bacterial decomposition of the fleshy parts, washing, and reweighing. The difference in these weighings will provide the biomass. This, together with mean annual temperature data and a knowledge of the life-cycle, will allow rough approximations of production.

AMPHIPODS

These seem to be most important in Chester Morse, especially in the profundal regions. Unlike the previous groups we can safely assign the classification of *Pontoporeia affinis* owing to the fact that it is the only recognized species in this genus and this genus is one of the very few species inhabiting only deep, cold, oligotrophic northern lakes (Pennak 1953). They occur in both planktonic and benthic habitats. Fish predation is their major source of natural mortality and to avoid it they mostly come out at night. Thut (1966) has reported *P. affinis* in Lake Washington; however, we have found an insignificant number at our stations. *P. affinis* has instars as do the chironomids. Therefore, similar methods will be used to calculate biomass and production as for the dipterans.

OTHER GROUPS

All other groups were found in such small numbers that it is doubtful that production estimates would be meaningful. This includes the Sialidae, the Ceratopogonidae, the Trichoptera, the Ephemeroptera, the Hydracarina, the Gastropoda, and the Hirudinea. Biomass will be obtained by direct weight. It will be seen that these organisms comprise a very small percent of the total standing crop of invertebrates. These are all found mainly in the littoral regions of the lakes (Table 1) and if more sampling were done in these areas, undoubtedly these macroinvertebrates would take on more importance.

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Table 1. Macrobenthos populations sampled from March to October 1973 on a regular basis in Lakes Washington, Sammamish, Chester Morse, and Findley.

Date	Station no	Number of samples	equip.	Chironomids	Oligochaetes	Amphipods	Sphaerids	Other groups	Debris wt (g)	
									refractile	nonrefractile
<u>1973</u>										
<u>LAKE WASHINGTON</u>										
7 Mar	1	3	VVS ^a	4	26			1 snail		
	2	3	VVS	112	426			1 C. pupae	0.28	0.01
	6	3	VVS	3	17			3 leeches		
	7	3	VVS	2	9			1 mite	94.0	0.17
	4	3	VVS	25	6	1		1 C. pupae	2.5	
	5	3	VVS	10	13		2	2 C. pupae		
	3	3	VVS	10	2					
20 Apr	2	5	VVS	76	32	1	18	2 C. pupae		
	1	5	VVS	2	4		2			
	5	5	VVS							
10 May	1	2	VVL ^b		5			1 shrimp(?)	16.4	
	2	2	VVL	59	12		15		1.9	
	5	2	VVL	2	2		1		1.5	
	6	2	VVL	9	20			5 leeches	1.9	
	8	2	VVL	85	7		9	3 leeches, 1 snail, 1 Chaoborus	47.1	
			↓							
				(42 metals - wt: 0.21683 g)						
15 Jun	1	2	VVL		2		5	1 snail	9.2	
	2	2	VVL	37	17		9		17.9	
	5	2	VVL				3		6.9	
	6	2	VVL		1		4	1 leech	13.6	
	8	2	VVL	63	2		3		93.7	
			↓							
				(26 metals - wt: 0.216100 g-used for Pb)						
31 Jul	2	2	VVL	217	432	7	3	1 mite, 1 snail, 2 leeches (small)	7.4	

Table 1 (cont.).

Date	Station no	Number of samples	Equip.	Chironomids	Oligochaetes	Amphipods	Sphaerids	Other groups	Debris wt (g)	
									refractile	nonrefractile
1973 LAKE SAMMAMISH										
13 Apr	2	4	E	144 64 (taken for metal analysis)	71			1 C. pupae	11.8	
	1	5	E	136 115 (taken for metals-wt: 0.1775 g)	14			1 C. pupae		
27 Apr	1	2	E	134 115 (taken for metals-wt: 0.268159 g)	57					
	2	1	E	24	27				10.2	
11 May	2	3	E	132	34		1	1 cerat	38.6	0.05
	1	2	E	86 ↓ (72 metals - wt: 0.061539 g)	5					
14 Jun	1	3	E	113 ↓ (14 metals - wt: 0.081881 used for lead)	10					
25 Jun	1	2	E	113 ↓ (25 metals - wt: 0.118794 g, used for Pb)	38	2				
	2	2	E	29	76				19.6	
13 Jul	1	3	E	174	42					
	2	3	E	41	129	2			22.1	0.3 (benthic algae)

Table 1 (cont.).

Date	Station no	Number of samples	Equip.	Chironomids	Oligochaetes	Amphipods	Sphaerids	Other groups	Debris wt (g)	
									refractile	nonrefractile
31 Jul	6	2	VVL	83	13		1		2.3	
	1	2	VVL	38	6					
	8	2	VVL	18	1		2	2 snails, 8 leeches (small)	32.4	
24 Aug	1	2	VVL	32 (13 m)†	10		1			
	2	2	VVL	111 (52 m)	186	1		1 mite	8.2	
	5	2	VVL	71 (15 m)	1	4	2	3 leeches	1.7	
	6	2	VVL	66 (19 m)	14			13 leeches (+ ~ 10 babies)	8.4	
	8	2	VVL	63 (25 m)	5		6	2 mites, 2 snails, 6 leeches	123.9	
25 Sep	8	2	VVL	53	5		7	19 leeches, 2 snails	92.6	
	6	2	VVL	67 (35 m)*	13		1	5 leeches	1.3	
	5	2	VVL	106 (40 m)*	2	4			6.2	
	1	2	VVL	35 (26 m)*	2				0.8	
	2	2	VVL	741 (250 m)*	601	18	15	1 snail	9.1	0.11
26 Oct	6	2	VVL	95 (24 m)† (34 m)*	7			1 snail, 5 leeches	5.9	
	1	2	B	27 (16 m)* (36 m)*	1					
	5	2	B	155 (31 m)	5	1		2 leeches, 1 mysid shrimp	2.5	
	2	2	B		236	1	3	4 mites	10.7	

Table 1 (cont.).

Date	Station no	Number of Samples	Equip.	Chironomids	Oligochaetes	Amphipods	Sphaerids	Other groups	Debris wt (g)	
									refractile	nonrefractile
2 Aug	1	4	E	326	57					
	3	4	E	72	29		9	1 snail, 1 may fly, 1 sialid	25.8	
10 Aug	1	4	E	317	41				0.2	
	4	4	E	9	3			3 caddis	0.2	
				[71 taken for analysis (data p.) used for Pb]						
21 Aug	1	4	E	212	127					
	3	2	E	100	34		1	1 sialid, 1 mite	36.7	
				(wet wt of 4.4446 g used for Hg)						
6 Sep	1	4	E	318(281 m)	82				1.9	
	3	2	E	208(88 m)	26	3	3	2 sialids, 12 mites, 1 caddis, 5 may	32.3	
28 Sep	1	4	E	356(245 m)	94				0.7	
17 Oct	3	2	E	104(54 m)	3		11	25 mites, 1 cerat, 8 unknown, 2 caddis	16.2	
	1	4	E	261	72					
<u>1973</u>				CHESTER MORSE LAKE						
3 Apr	1	1	E	0	2	10				
17 Apr	1	2	E	4	8	14			1.1	
	2	2	E	72	1	6	2	1 mayfly, 5 cerats	7.1	

Table 1 (cont.).

Date	Station no	Number of Samples	Equip.	Chironomids	Oligochaetes	Amphipods	Sphaerids	Other groups	Debris wt (g)	
									refractile	nonrefractile
1 May	1	3	E	7	8	22				
22 May	1	3	E	6	9	11				
	2	3	E	234	18	7	15	4 sialid, 1 mite	67.5	
20 Jun	1	2	E	4	11	7				1.2
	2	2	E	37	11		3	1 sialid	37.7	
10 Jul	1	3	E	6	13	20		1 ceratogonid		
	2	3	E	24	30		7	3 sialids, 1 mite	52.5	
24 Jul	1	3	E	3	4	10				
	2	4	E	101	108		129	2 caddis, 2 sialid, 2 leeches, 3 snails	1.7	
14 Aug	1	4	E	21	35	61				10.4
	2	4	E	6	76		121	2 mites, 10 leeches, 2 caddis, 2 sialids, 6 cerat	5.6	
28 Aug	1	4	E	12	13	32	5		0.3	1.2
	2	4	E	42	95	1	129	15 mites, 9 leeches, 1 sialid, 3 caddis, 17 cerat	53.9	0.9
11 Sep	1	4	E	17	26	72			4.3	
	2	4	E	144	277	12	177	8 sialids, 8 caddis, 17 cerats, 11 leeches, 38 mites	21.8	

Table 1 (cont.).

Date	Station no	Number of Samples	Equip.	Chironomids	Oligochaetes	Amphipods	Sphaerids	Other groups	Debris wt (g)	
									refractile	nonrefractile
8 Oct	1	4	E	34 (16 m)*	10	61			1.1	
	2	4	E	101	85		103	4 leeches, 4 mites, 22 caddis, 10 cerats, 6 sialids	6.9	
<u>1973</u>				FINDLEY LAKE						
24 May	2	2	E	361	40		45	2 caddis, 1 sialid, 2 mites, 3 cerats, 1 simuliid(?)	46.4	
7 Jun	2	3	E	113	22		21	3 caddis	1.7	
	1	3	E	15	1				7.7	
5 Jul	2	2	E	27	3		3	1 mayfly, 1 cerat	3.8	
	1	2	E	109 ↓ (40 for metals - wt: 0.038888 g, used for Pb)	17				3.9	
26 Jul	1	3	E	213	26				5.2	
	2	4	E	67	8		77	5 sialids, 3 caddis	31.6	
30 Aug	1	4	E	261 (251 m)+	91				55.2	
	2	4	E	132	1		39	9 sialids, 6 caddis, 10 may	5.9	
13 Sep	2	4	E	226 (125 m)	21		105	6 sialids, 13 cerats, 15 caddis, 6 snail, 4 may, 1 mite	20.7	
	1	4	E	110 (59 m) ↓ (wet wt: 0.9713 g)	32			1 caddis	2.2	

Table 1 (cont.).

Date	Station no	Number of Samples	Equip.	Chironomids	Oligochaetes	Amphipods	Sphaerids	Other groups	Debris wt (g)	
									refractile	nonrefractile
3 Oct	1	4	E	166(90 m) [†]	23		1		2.1	
	2	4	E	167	3		83	7 sialids, 11 may, 3 cerats, 1 mite	9.7	

^aArea of VVS = 0.01 m².

^bArea of VVL = 0.1 m².

*Used for Hg.

†Used for Pb.

Table 2. Bottom types of Lakes Washington, Sammamish, Chester Morse, and Findley at stations sampled for macrobenthos populations from March to October 1973.

Lake	Station	Bottom type
Lake Washington	1	Soft, fine mud, little large debris (60 m)
	2	Silt plus heavy debris from the Cedar River (15 m)
	3	Moderate amount of large debris mixed with mud (10 m)
	4	Moderate amount of large debris mixed with mud (10 m)
	5	Moderate amount of large debris mixed with mud (10 m)
	6	Moderate amount of large debris mixed with mud (10 m)
	7	Mostly bark and woody material, little mud (18 m)
	8	Mostly bark and woody material, little mud (18 m)
Lake Sammamish	1	Soft, fine mud, usually black (25-30 m)
	2	Little mud, bark and woody material predominant (8 m)
	3	Little mud, bark and woody material predominant (8 m)
	4	Silt and a lot of sand (4 m)
Chester Morse	1	Fine mud, little large organic debris (34 m)
	2	Little mud, large bark and refractile fraction (8 m)
Findley Lake	1	Fine mud, small organic debris fraction (27 m)
	2	Sandy, moderate amount of organic debris (3 m)

Table 3. Parameters and percent variation explained by length using the one-parameter model, weight = aL^3 , and the two-parameter model, weight = aL^b . Data used was for station 1 at Findley Lake on 30 August 1973.

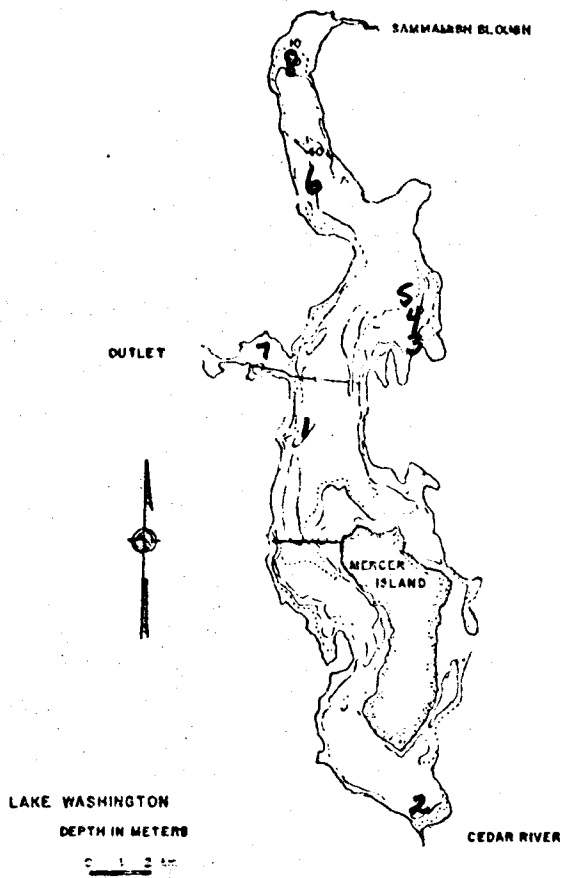
Model	Weight	a	b	Percent variation explained by length
2 parameter	wet	2.47431×10^{-6}	3.1666	87.8
1 parameter	wet	3.93554×10^{-6}		87.7
2 parameter	dry	1.44370×10^{-9}	5.1595	90.0
1 parameter	dry	6.09011×10^{-7}		82.4

Table 4. Turnover ratios derived from direct estimates of production and mean standing crop.

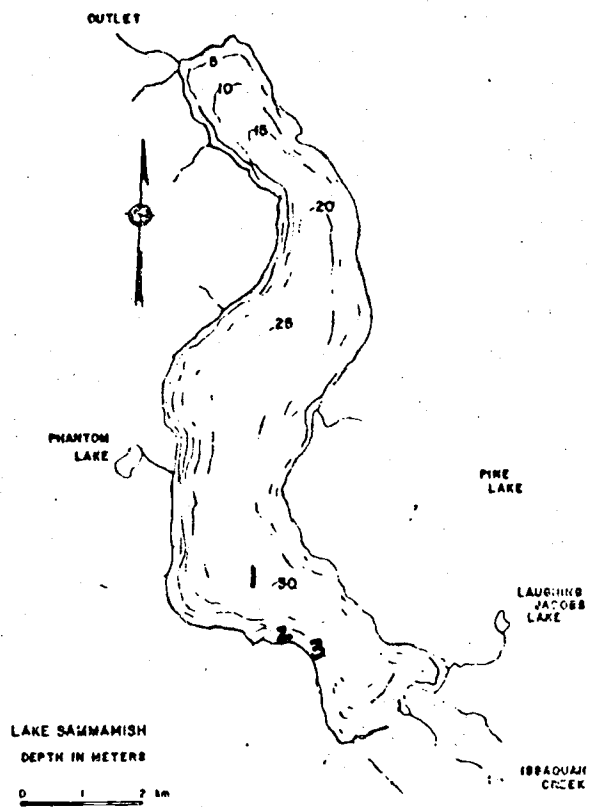
Organism	Water	Annual TR	Number of generations	Life-cycle TR	Authority
Chironomidae	lake, littoral	8-9	1-2	5 ^a	Miller 1941
Chironomidae	lake, profundal	2-3	1/2-1	4 ^a	Miller 1941
<i>Tanytarsus jucundus</i>	lake	3.4 ^b	1	3.4 ^b	Anderson Hooper
<i>Calopsectra dives</i>	spring	3.5 ^b	1	3.5 ^b	Teal 1957
<i>Analopymia dyari</i>	spring	2.7 ^b	1	2.7 ^b	Teal 1957
<i>Corixa germari</i>	reservoir	2.5 ^b	1	2.5 ^b	Crisp 1962
<i>Bactis vagans</i>	stream	9.7	3	3.2	Waters 1969
Chironomidae	lake, sublittoral	15	Several	5 ^a	Kajak and Rybak
Chironomidae	lake, profundal	3.8	1	3.8	Kajak and Rybak

^aApproximation.

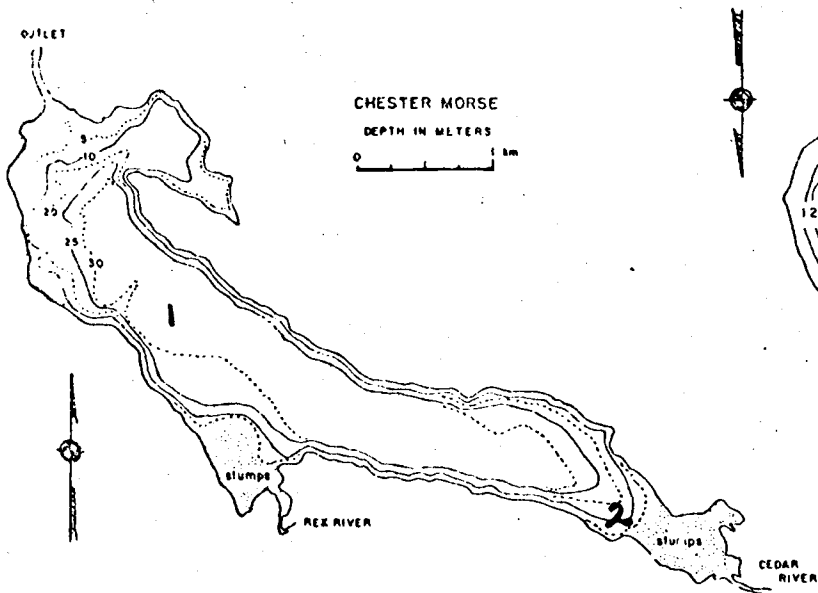
^bCalculated from author's data.



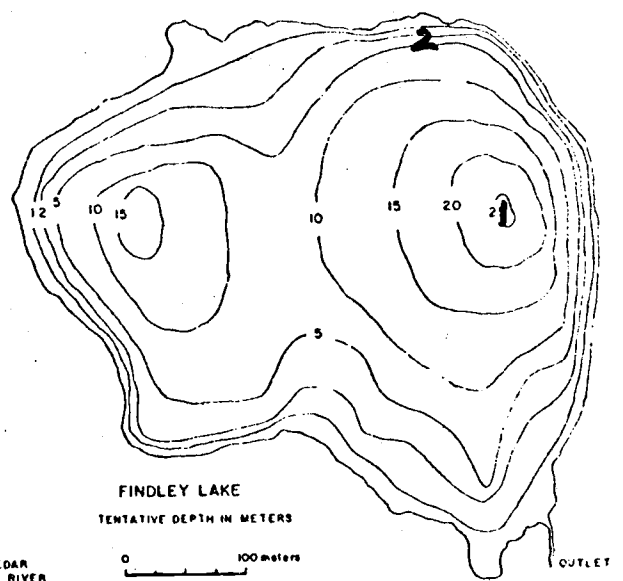
Map of Lake Washington.



Map of Lake Sammamish



Map of Chester Morse Lake.



Map of Findley Lake.

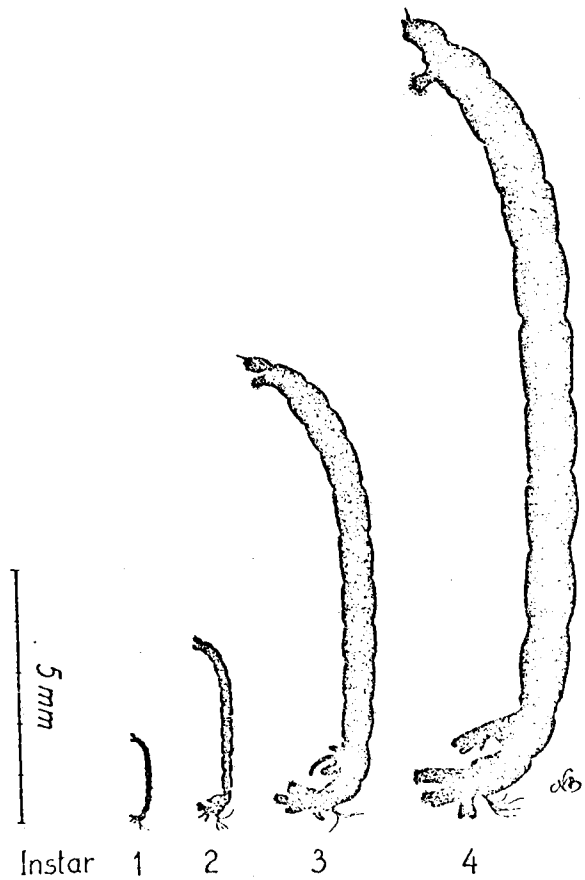


Figure 2.

Figure 1

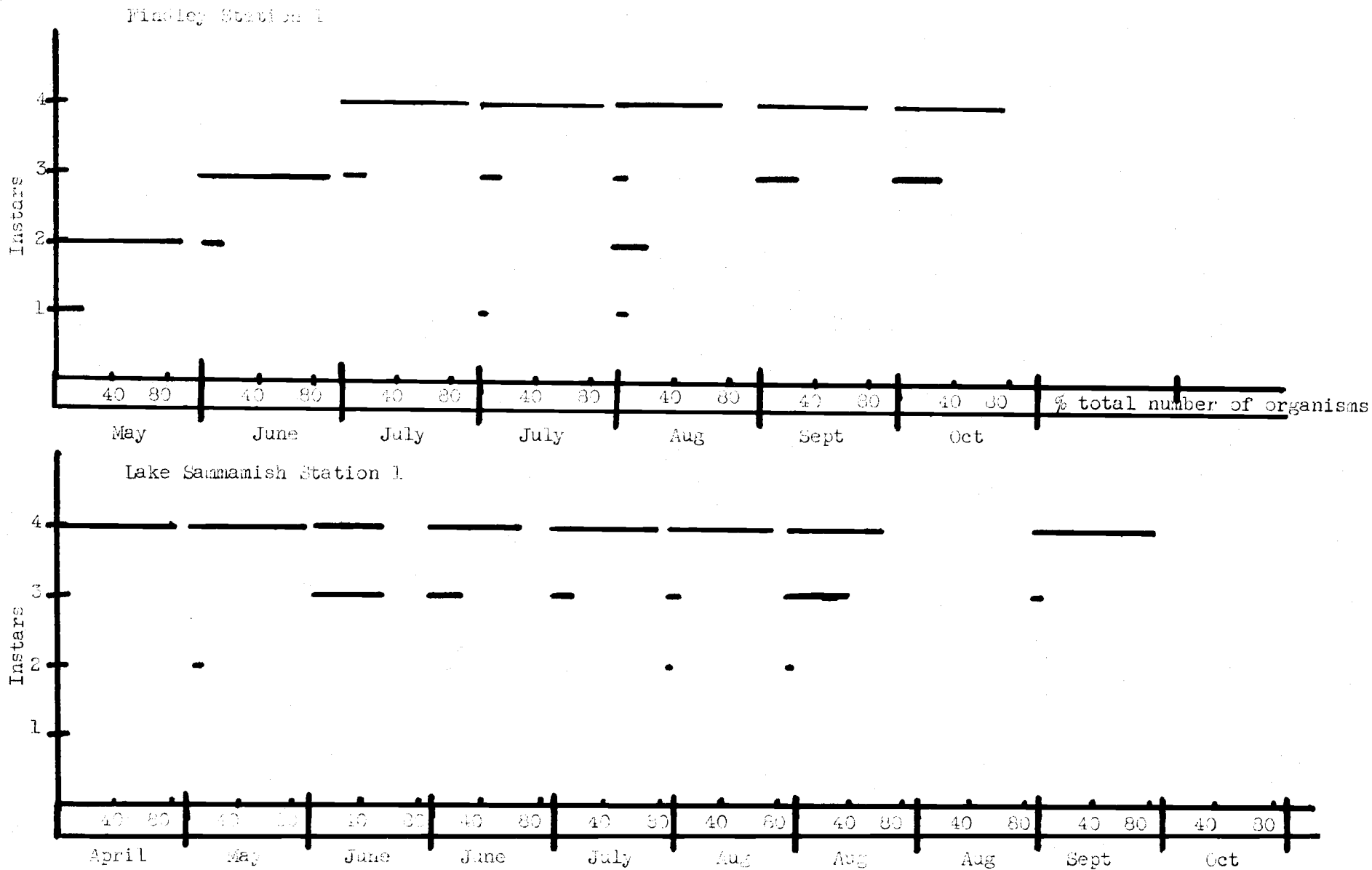
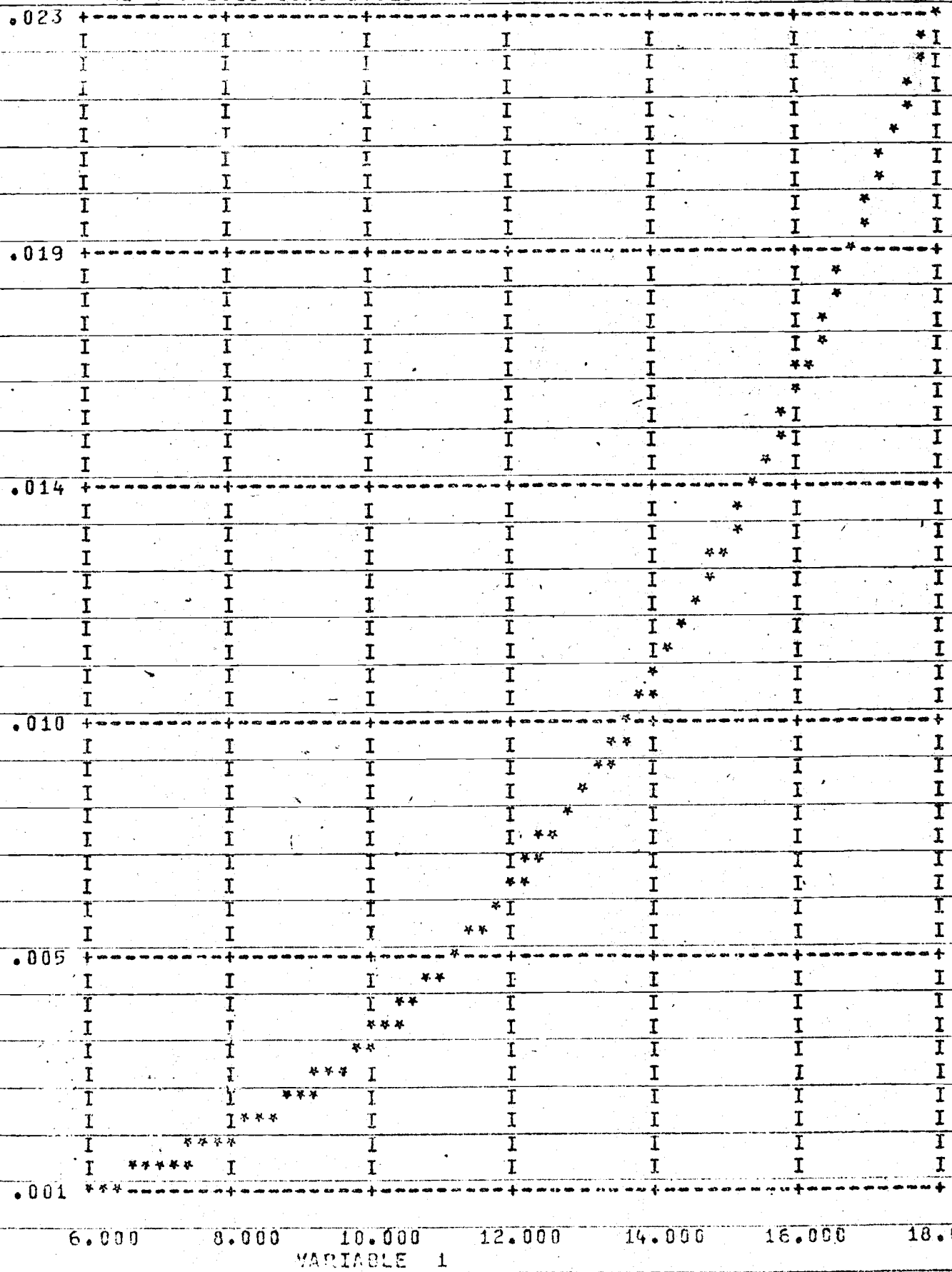


Figure 4

Findley Lake, two parameter model, wet weight.
 PLOT OF THE FUNCTION WITH RESPECT TO VARIABLE 1
 MEAN VALUES SUBSTITUTED FOR THE OTHER VARIABLES

FUNCTION

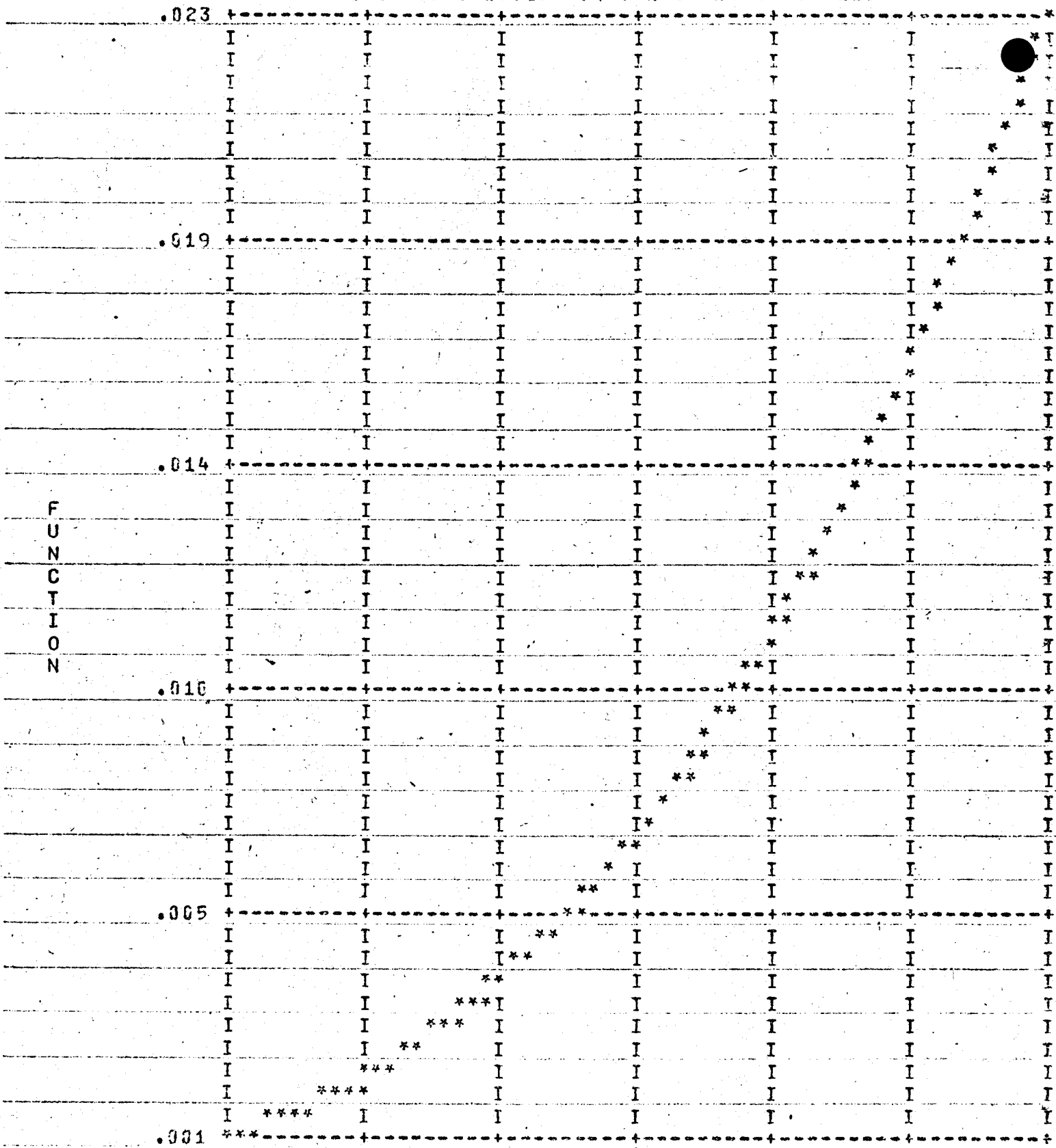


6.000 8.000 10.000 12.000 14.000 16.000 18.000
 VARIABLE 1

THE PARAMETERS BEING USED ARE
 2.47431E-06 3.1566
 MEAN VECTOR
 1 12.4400 9.744920E-03

Figure 5

Findley Lake, one parameter model, wet weight
 PLOT OF THE FUNCTION WITH RESPECT TO VARIABLE 1
 MEAN VALUES SUBSTITUTED FOR THE OTHER VARIABLES



6.000 8.000 10.000 12.000 14.000 16.000 8%

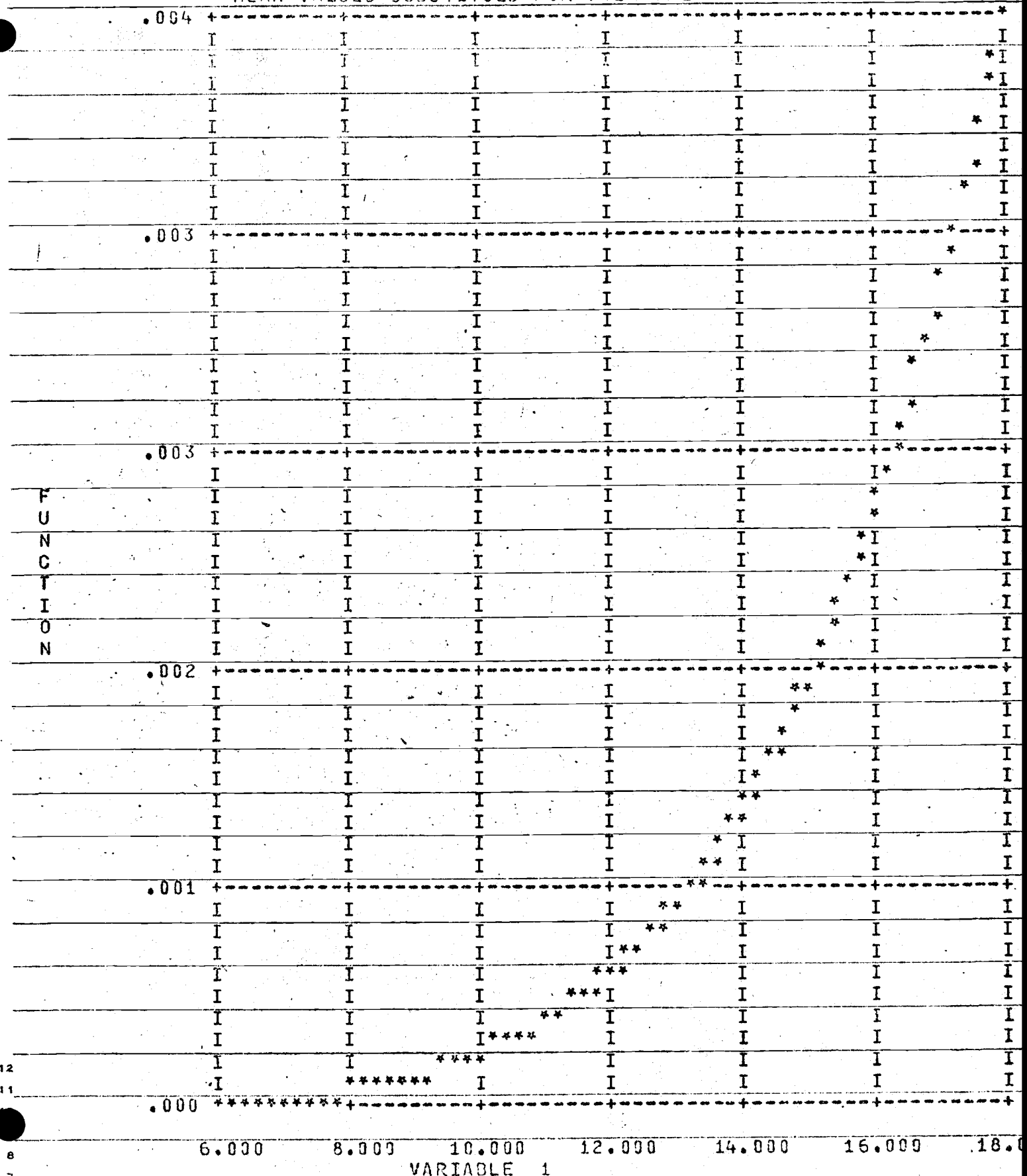
VARIABLE 1

THE PARAMETERS BEING USED ARE
 3.93554E-06

MEAN VECTOR
 1 12.4400 9.7449205-03

Figure 6

Findley Lake, two parameter model, dry weight.
 PLOT OF THE FUNCTION WITH RESPECT TO VARIABLE 1
 MEAN VALUES SUBSTITUTED FOR THE OTHER VARIABLES



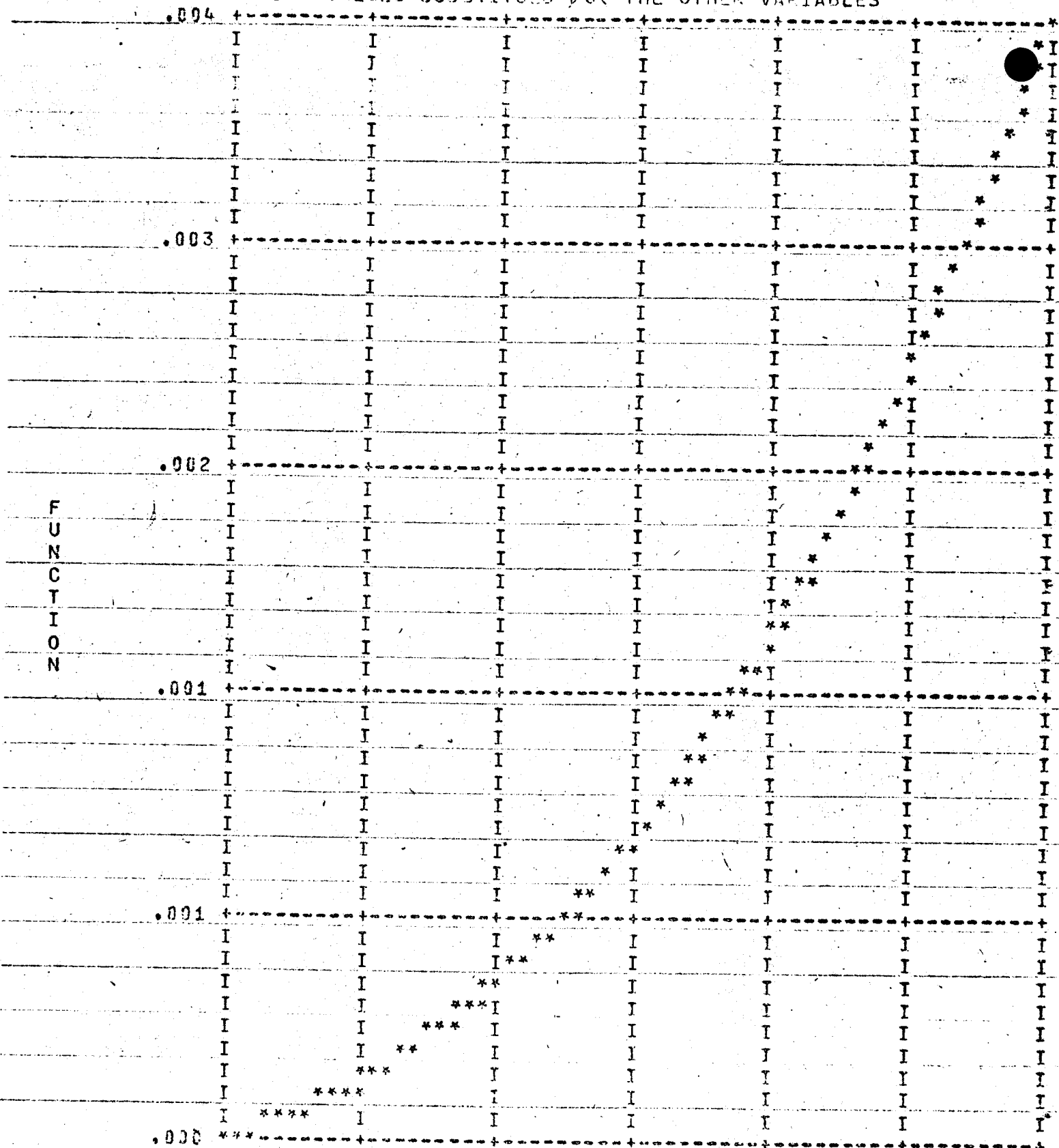
THE PARAMETERS BEING USED ARE
 1.44370E-09 15.1595 /

MEAN VECTOR

Figure 7

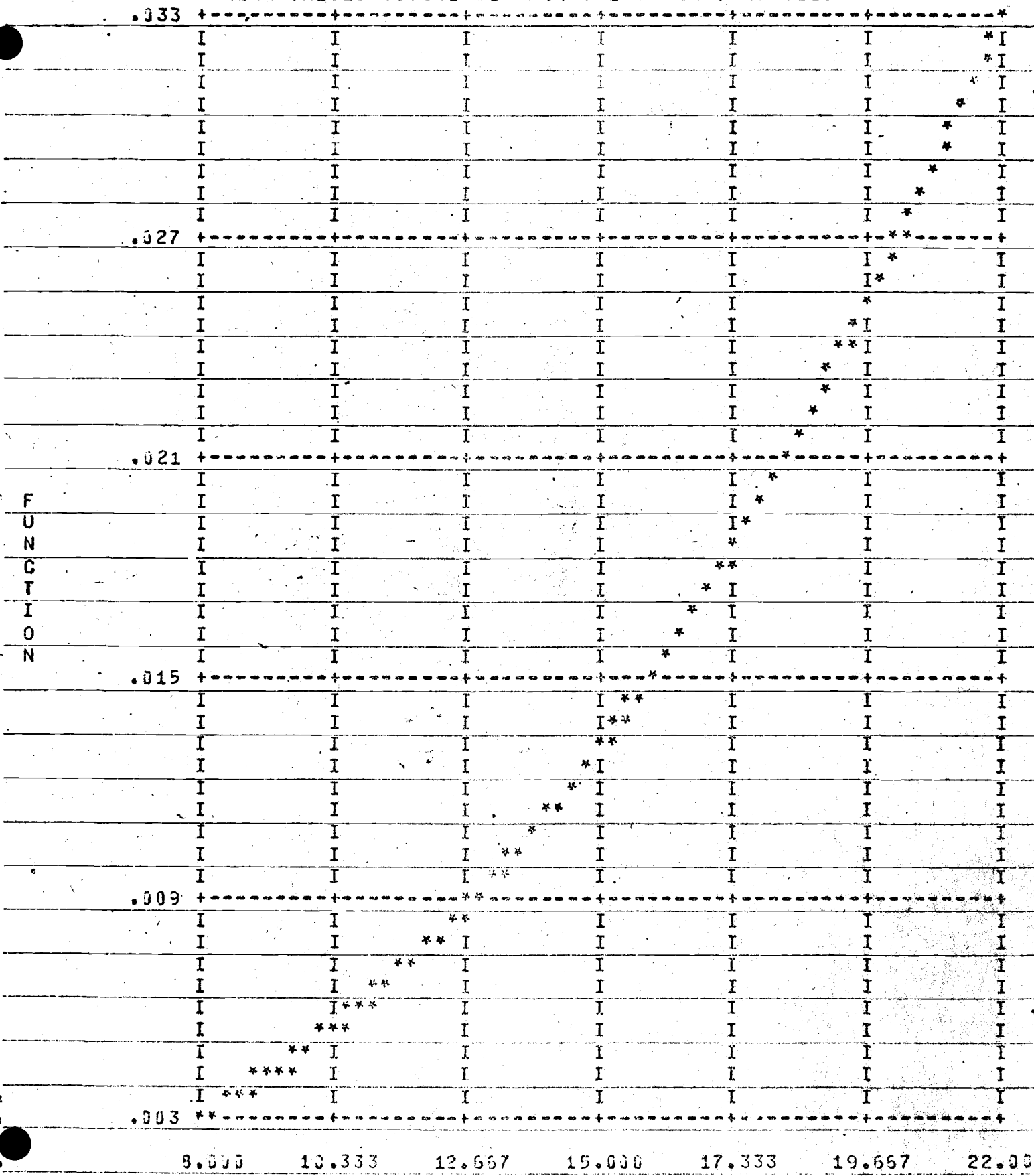
1 12.4400 1.355280E-03

Pinney Lake, one parameter model, dry weight.
 PLOT OF THE FUNCTION WITH RESPECT TO VARIABLE 1
 MEAN VALUES SUBSTITUTED FOR THE OTHER VARIABLES



6.000 8.000 10.000 12.000 14.000 16.000 18.000
 VARIABLE 1
 THE PARAMETERS BEING USED ARE
 6.09511E-07
 MEAN VECTOR
 1 12.4400 1.395280E-03
 Figure 8

Sammamish, two parameter model, wet weight.
 PLOT OF THE FUNCTION WITH RESPECT TO VARIABLE 1
 MEAN VALUES SUBSTITUTED FOR THE OTHER VARIABLES

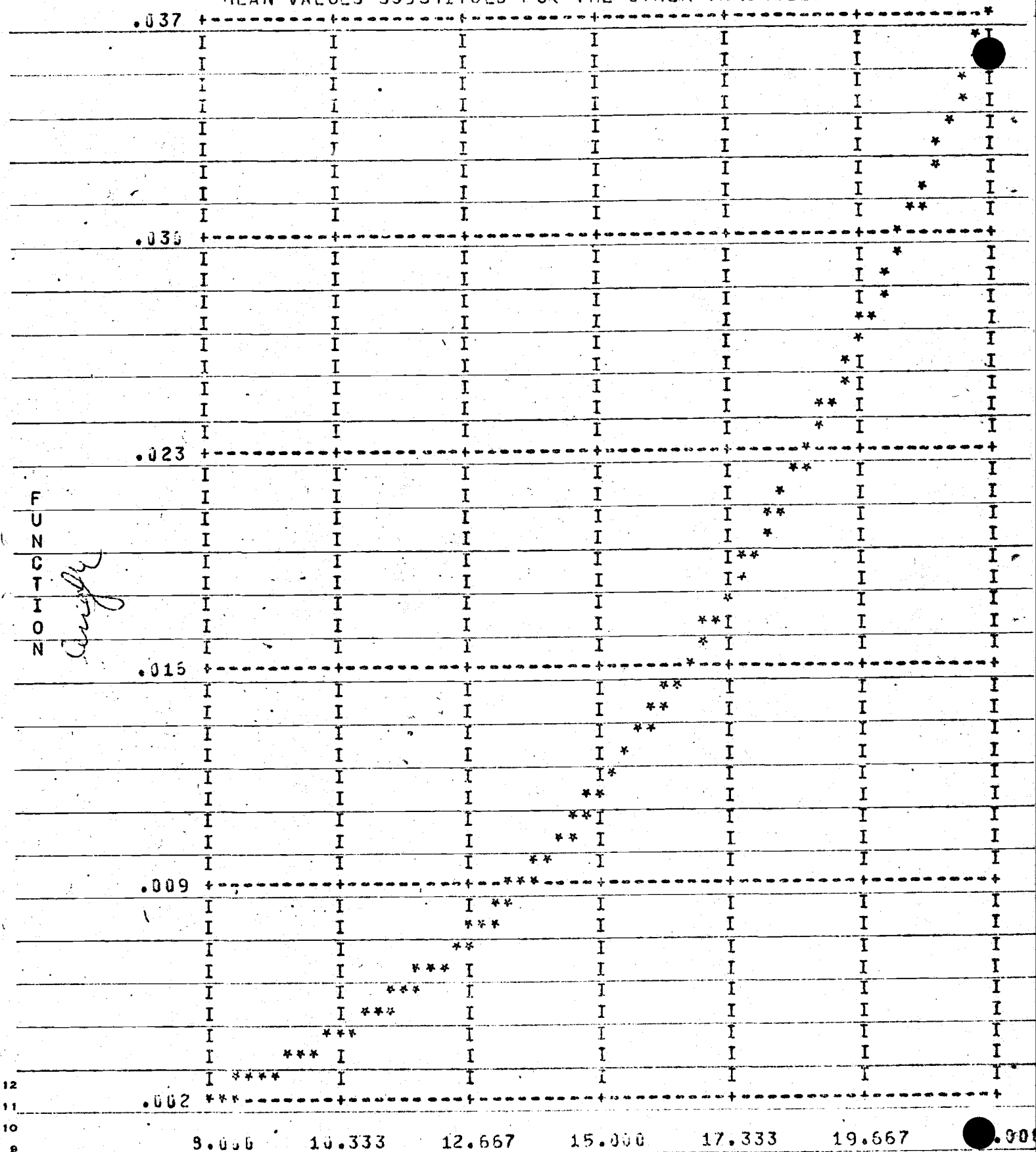


THE PARAMETERS BEING USED ARE
 1.74835E-05 2.4031
 MEAN VECTOR
 1 15.465 1.49198E-02

Figure 9

Sammamish, one parameter model, wet weight.

PLOT OF THE FUNCTION WITH RESPECT TO VARIABLE 1
 MEAN VALUES SUBSTITUTED FOR THE OTHER VARIABLES



FUNCTION

Verify

12
11
10
9
8
7
6
5
4

9.000 10.333 12.667 15.000 17.333 19.667 .00

VARIABLE 1

THE PARAMETERS BEING USED ARE

3.49453E-06

MEAN VECTOR

1 15.4600

1.49986E-02

Figure 10

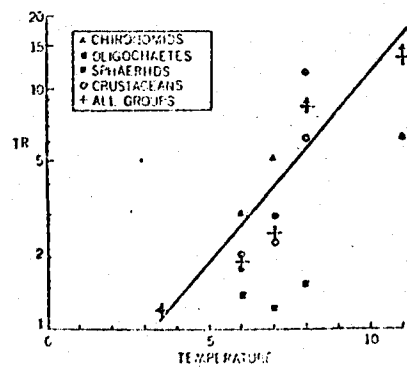
Sammamish, two parameter model, dry weight.
 PLOT OF THE FUNCTION WITH RESPECT TO VARIABLE 1
 MEAN VALUES SUBSTITUTED FOR THE OTHER VARIABLES

48

FUNCTION	0.001	0.002	0.003	0.004	0.005	0.006	0.007	0.008	0.009	0.010
1	I	I	I	I	I	I	I	I	I	I
2	I	I	I	I	I	I	I	I	I	I
3	I	I	I	I	I	I	I	I	I	I
4	I	I	I	I	I	I	I	I	I	I
5	I	I	I	I	I	I	I	I	I	I
6	I	I	I	I	I	I	I	I	I	I
7	I	I	I	I	I	I	I	I	I	I
8	I	I	I	I	I	I	I	I	I	I
9	I	I	I	I	I	I	I	I	I	I
10	I	I	I	I	I	I	I	I	I	I
11	I	I	I	I	I	I	I	I	I	I
12	I	I	I	I	I	I	I	I	I	I

3.333 10.333 12.667 15.000 17.333 19.667 22.000
 VARIABLE 1
 THE PARAMETERS BEING USED ARE
 0.210000-07 2.9339
 MEAN VECTOR
 1 10.7500 2.104640E-03

Figure 11



Relation between annual mean temperature (C) and the turnover ratio (TR) of the macroinvertebrate community and of broad taxonomic groups.

Figure 13