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Causal Analysis of Some Biological Data on *Illex illecebrosus*

by

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Introduction

Research on squid populations in the Northwest Atlantic has provided a wide range of biological data. Growth, food type, feeding patterns, migration and abundance have been described (Lu 1973; Amaratunga 1890a; b; Hirtle et al. 1981) but the interaction between various biological factors remains unclear. The effects of size, maturity stage and stomach fullness on abundance are particularly intriguing. These data are routinely collected by the Molluscan Section of the Department of Fisheries and Oceans, Canada and the utilization of the additional information on abundance contained in these measurements is desirable.

Large apparent fluctuations in abundance, as indicated by the size of the catch, have been observed in recent years. The increasing importance of the fishery for Illex illecebrosus has been used to explain some of this variation. In addition, recent work has employed temperature as an explanatory variable for abundance fluctuations (Mohn 1981). Because a one year life cycle is usually assumed for this species, the prediction of abundance is problematic. Also, problems occur in the estimation of catch per unit effort, the standard abundance indicator, due to the difficulty of assigning effort to the overall squid catch. These problems emphasize the need to extract causal relationships between abundance and various biological indicators.

A review of the literature related to cephalopod biology gives us some understanding of the probable causal effects of temperature on several biological factors. Loligo vulgaris from the NE Atlantic is supposed to be temperature dependent in regard to spawning period, migration starting dates and abundance (Timbergen and Verwey 1945). Todarodes sagittatus also in the NE Atlantic, probably migrates south to spawn in warmer waters (Wiborg pers. comm.). In fact, mature animals were collected in Portugese deep waters (Coelho 1981). The distribution of Todarodes pacificus was found to be temperature related (Hamabe 1974). Richard (1971) concluded that temperature seemed to be the main factor influencing growth success in Sepia officimalis. Also, a relationship was found between temperature and longevity. Boletzki (1973) noted for Illex coindeti the existence of a temperature range for survival. Illex illecebrosus larval development, fertilization efficiency and spawning success were found to be temperature dependent (O'Dor et al. 1981; 1982). Field data analyzed from Illex illecebrosus also illustrated a relationship between the arrival and departure dates from inshore areas (Dupouy 1982). Fedulov (1980; 1981) related temperature anomalies with arrival dataes of I. illecebrosus on the Scotian Shelf. These are in summary the supporting arguments which brought us to choose the variables for the present study.

In this paper we analyse the variation in abundance for the three year period 1979-1981. These years were chosen as representative of high, medium and low abundance. We consider maturity stage, size and stomach fullness as biological variables potentially causally related to mean catch/day as an indicator of abundance during the period when squid is available to the fishery.

In addition, the effects of temperature and timing (i.e. temporal factors such as photoperiod) as general abiotic factors were included in the analysis.

A basic premise in our analysis is that the biological and environmental variables interact and so may effect abundance and each other both directly and indirectly. Path analysis, developed by Wright (1934) and well described by Li (1975) is designed to examine such systems where direct and indirect causal paths may be important. Here we hypothesize several models for the interactions between and among the biotic and abiotic variables and examine these hypotheses with path analysis.

Material and Methods

Three years of data on maturity stage, mean mantle length, sex ratio, mean stomach fullness and mean number of individuals caught per day in the international offshore fishery were used. The biological data base was obtained from research vessel surveys and observers on the international fleet for 1979-1981 on the Scotian Shelf. Mean surface temperatures were obtained from ST contours of the shelf. These values were available on a weekly basis from Canadian Metoc Center data. Temperature values at depth were not available corresponding to all locations where samples were collected. Surface temperature was considered to be the most consistent data to define temperature variation through each year for the area examined (Appendix 1). We aggregated the data on a monthly basis and utilized the July to November period which corresponds to the main fishery season for squid.

The mean maturity was calculated on a weekly basis as the mean stage of animals sampled whose maturity was greater than stage zero. The animals were staged following the maturity scale described by Durward et al. (1978) for females and Mercer (1973) for males. The data were later aggregated on a monthly basis. The mean stomach fullness was similarly calculated.

Animals were coded with reference to the scale described by Amaratunga et al. (1980b). Sex ratio was defined as the number of males devided by the number of females. Initially, we calculated all means for the sexes separately. However, there was no significant difference between the means (T-test, alpha=.05) and so the sexes were combined to simplify the analysis. Table 1 shows a summary of the data used.

Summary of Statistical Methods

Laboratory experiments are designed to allow certain factors of interest to be considered under control. With field data, statistical tools are needed to point out the effects of different variables. Partial correlations can be used to examine the correlation of A_1 with A_2 holding $A_3 \ldots A_n$ constant. A study to simultaneously intercorrelated variables in a causal scheme presents greater complexity for statistical analysis. Rather than considering only correlations between variables, path analysis utilizes partial regression coefficients to allow the consideration of the influence of interacting variables in a hypothesized causal scheme. A path is a route connecting two variables and may be direct, with no intermediate variables or compound, i.e., indirect, with several component paths and intermediate variables. These partial regression coefficients are called path coefficients and have a causal interpretation because they are directional. In addition, if the variables are standardized to zero mean and unit variance, inferences can be made concerning the relative importance of various pathways to a variable. We use standardized variables throughout this study. The values obtained for such path coefficients can only be considered with respect to a specific point of view expressed by a diagram representing each hypothesized causal structure. General rules are followed to read these diagrams:

1) Cause and effect relationships are unidirectional and are shown by arrows with the head at the dependent

variable. Correlations, implying no causality are shown with a double headed arrow.

2) All the hypothesized factors (predictors) contributing to the total variation of the dependent variable are dαawn in. Then, all the factors not included in the diagram will be included in a residual factor which is a composite of the unknown sources of variation. The residual coefficients are indicated here by a double line with no arrow.

3) The overall coefficient for a compound path is the product of the coefficients of its component paths.

4) The correlation between two variables is the sum of all the paths by which they are connected.

5) The amount of variance explained by the model for any dependent variable is the sum of all complete circuits among the independent variables affecting that dependent variable. Alternatively, this can be calculated as one minus the square of the coefficient of the residual factor.

In comparison, multiple regression would be represented by a very simple path diagram hypothesizing only direct relationships between the dependent and independent variables (with no compound paths). For a full description of the path analysis method see Li (1975).

Results and Discussion

Our first step was to perform a stepwise multiple regression using the selected biotic and abiotic variables as predictors for catch (abundance). This analysis indicated that only the month of the year and mean surface temperature explained significant proportions of the total variance at the .10 level (Appendix II). Figures 1, 2, 3 and Table 2 show the regressions obtained for size and maturity and gut fullness indices between the sexes.

We then proceeded to hypothesize several path diagrams relating the variables. A correlation matrix of the variables (Appendix 2) is useful in examining these diagrams.

Pathways Relating Biotic and Abiotic Factors

1) Path Diagram 1

a) Size related to month and temperature

In this path diagram we hypothesize that size is affected by temperature and month and each of these directly and indirectly effect maturity. In this scheme, month and temperature have a strong positive effect on size. But, because of the negative path coefficient between month and temperature, we see that there is a compound pathway from month through temperature to size with a negative sign overall. This uses the rule that the coefficient for a compound path is the product of the coefficients of its component pathways. So, the effect of month on mean size of squid during its presence on the shelf is mediated by the declining surface temperatures observed during the period under study.

b) Maturity - Here, maturity increases with both month and size, with the month having the stronger effect. Temperature appears to have a slight negative direct effect. However, temperature effects on size and hence on maturity have an overall positive sign. The indirect effects of time on maturity (month mediated by size, month mediated by temperature) are all positive reflecting the progress of the maturation process over the study period. If we consider the three component path, month/temperature/size/maturity, we observe a small negative effect which may indicate that the maturation process is balanced by the size of the animal and the environmental conditions, including the daylight changes over the season.

2) Path Diagram 2

Here we have drawn the hypothesis which suggests the same effects as in the previous diagram but now on stomach fullness. This hypothesis was drawn to examine the relationship between the occurrence of recently feeding animals and their size considering also the influence of temperature and time. In Diagram 2 we see that the direct effects of temperature and month are strongly negative but size and the two indirect pathways (month/size/gut and temperature/size/gut) as well as month through temperature to gut are all strongly positive. In summary, there appears to be a balance between the mean size effect on feeding and the direct temperature and monthly effect, which may be indicative of the physiological effects of changing temperature and photoperiod on feeding.

Pathways Relating Abundance to Biotic and Abiotic Factors

3) Path Diagram 3

The hypothesis is to relate stomach fullness, maturity, and size of animals with abundance. The scheme proposed in this diagram explains 84% of the observed variation in the abundance index. Both direct and indirect paths from maturity to abundance are strongly negative. This seems to be caused by the fact that as the animals grow and mature over the period considered, they are also leaving the study area. The positive direct effect of stomach fullness on catch is greatly reduced by the indirect effects through maturity and size. This means that the occurrence of animals with full stomachs in the catch is also a reflection of the size of the animals and their maturity stage.

4) Path Diagram 4

Here the hypothesis is to include temperature effects with size and maturity of squid on abundance. As in the previous hypothesis the negative coefficients from size and maturity to abundance are relatively large. Now we can see that the direct effect of temperature is very small. However, note that the indirect effects of temperature through the biological variables are quite important. Both of these indirect pathways have positive effects on abundance. From this we can see that the correlation between temperature and abundance is in fact due to the temperature effects on growth and the maturation processes.

5) Path Diagram 5

We summarize in this diagram many of the relationships found in the other schemes. The interactions of size, temperature and maturity are as previously noted. In addition, it is apparent that the abundance and the stage of maturity of squid strongly effect their feeding. Abundance seems to be the dominant or key variable here, suggesting a density dependent mechanism. However, the high coefficient from catch to gut would probably be reduced by a direct temperature gut pathway on the mechanism of month in this diagram. The indirect negative effect of maturity through abundance to gut fullness balances the direct effect of maturity stage. As the animals increase in size, abundance decreases probably as a result of emigration to inshore feeding areas or later in the season south to the spawning grounds. This is also reflected in the lower gut fullness of the animals as abundance declines on the fishing grounds through the season. In general, the strong effect of abundance on feeding may be due to the importance of schooling behavior for feeding strategies or the potentially high incidence of cannibalism reported for this species (Amaratunga 1980b).

6) Accessory Path Diagrams

In appendix 3 we present some simple diagrams (B,D,F) to examine the interaction of temperature on catch, directly and indirectly through size, maturity or gut fullness. Also the direct influence of catch on each, size, maturity and gut fullness is diagrammed (A,C,E) to investigate the possibility of density dependence. These three sets of diagrams seem to indicate a reciprocal relationship between abundance and the biological factors. Reciprocal relationships in path analysis are more complex to analyse but such further work is needed in light of these hypotheses.

If now we compare the results from the multiple regression approach (Appendix II) with our path analysis we can see that the former, while explaining an equivalent amount of the variation in catch, gives little information about the mechanism underlying the explanatory power of any independent variable. This is most clearly seen with the temperature effect. Path analysis has shown that temperature is important to abundance variation because of its effects on the mean size and maturity stage. We can further hypothesize from this that the temperature is affecting the growth and maturation processes and these processes are importnat at least with regard to the distribution of squid on the fishing grounds. Similarly the effect of stomach fullness appears negligable in the multiple regression. However path diagram 5 indicates a trade off between abundance, feeding condition and maturation.

In conclusion, we would like to point out that our results from this analysis are consistent with the general understanding of the biology of squid, Illex illecebrosus. However, the analysis could be strengthened by an increased sample size and better indices in particular with regard to temperature, seasonality and abundance. We feel that the path analysis approach can indicate other important areas for further research such as the interaction of growth and maturation both spatially and temporally. This would contribute to the development of a better knowledge of squid life history.

Acknowledgements

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References

Amaratunga, T. (1980a). Growth and maturation patterns of the short-finned squid (Illex illecebrosus) on the Scotian Shelf. NAFO SCR Doc. 80/II/30, Serial No. N062, 17 pp.

Amaratunga, T. (1980b). Preliminary estimates of predation by the short-finned squid (Illex illecebrosus) on the Scotian Shelf. NAFO SCR Doc. 80/II/31, Serial No. N063, 13 pp.

Amaratunga, T., and R. D. Durward. A guide for data collection in the field for the squid, Illex illecebrosus. ICNAF Res. Doc. 82/II/5, Serial No. 5157.

Boletzky, S. V. et al. (1973). Spawning and development of the eggs in the laboratory of Illex coindetti, (Mollusca, Cephalopoda). Veliger 15, 256-257.

Dupouy, H. and J. P. Minet. 1982. Catch, effort and biological characteristics of squid (Illex illecebrosus) in the French Subarea fishery (Subdiv. 3Ps), in 1981. NAFO SCR Doc. 82/VI/19.

Durward, R. D., T. Amaratunga and R. K. O'Dor. 1978. Maturation index and fecundity for females Illex illecebrosus (Le Sueur, 1821). ICNAF Res. Doc. 78/II/1, Serial No. 5153.

Coelho, M. L. 1981. Núcleo cefalópodos. Relatorio de situação Rel. int. No. 9. INIP, Portugal.

Fedulov, P. P. and Yu. M. Froerman. 1980. Effect of abiotic factors on distribution of young shortfin squids, Illex illecebrosus (Le Sueur, 1821). NAFO SCR 80/VI/98.

Fedulov, P. P. and T. Amaratunga. 1981. On dates of shortfinned squid, Illex illecebrosus, immigration into the Scotian Shelf. NAFO SCR Doc. 81/VI/32.

Hirtle, R. W., M. E. Demont and R. K. O'Dor. 1981. Feeding, growth and metabolic rates in captive short-finned squid, Illex illecebrosus in relation to the natural population. Journal of Shellfish Research, Vol. 1, No. 2, pgs. 187-192, 1981.

Lu, C. C. 1975. Path Analysis - A Primer. Boxwood Press, Pacific Grove, California, 631 pp.

Lu, C. C. 1973. Systematics and zoogeography of the squid genus Illex (Oegopsida: Cephalopoda). Ph.D. Thesis, Memorial University of Newfoundland, St. John's, Newfoundland.

Mercer, M. C. 1973. Sexual maturity and sex ratios of the ommastrephid squid, Illex illecebrosus (Le Sueur), at Newfoundland (Subarea 3). ICNAF Res. Doc. 73/71.

Mohn, R. K. 1981. Indices of abundance and bottom temperature relationships for squid in Div. 4VWX. NAFO SCR Doc. 81/IX/99.

Mohn, R. K. 1981. Abiotic factors relating to squid abundance as determined from groundfish cruises, 1970-1980. NAFO SCR Doc. 81/VI/34, Serial No. N316.

O'Dor, R. K. et al. 1980a. Feeding and growth in captive squid (Illex illecebrosus) and the influence of food availability on growth in the natural population. ICNAF Sel. Pap. 6: 15-21.

O'Dor, R. K. et al. 1981. The embryonic development of the squid Illex illecebrosus in the laboratory. NAFO SCR Doc. 81/VI/29.

O'Dor, R. K. et al. 1982. Embryonic development of the squid, Illex illecebrosus and effect of temperature on development rates. J. Northw. Atl. Fish. Sci. Vol. 3: 41-45.

Tinberg, L. and Verwey, J. 1945. Zur. biologie von Loligo vulgaris. Arch. Neerl. Zool., 7(1-2).

Wright, S. 1934. The method of path coefficients. Annals of Mathematical Stat. 5: 161-215.

TABLE 1 – SUMMARIZED DATA USED IN THIS ANALYSES

VARIABLES MEAN VALUES (JULY-NOVEMBER) \ YEAR		1979	1980	1981
TEMPERATURE	$\bar{T}$	13.92	13.96	13.76
CATCH	$\bar{C}$	7.83	6.01	5.51
FEMALE SIZE	FL	247.03	214.92	200.22
MALE SIZE	ML	226.85	200.47	194.99
MEAN SIZE (mm)	$\bar{L}$	236.94	207.69	197.61
FEMALE MATUR.	MF	2.19	1.95	1.72
MALE MATUR.	MM	2.57	2.09	1.88
MEAN MATUR.	$\bar{M}$	2.38	2.02	1.80
FEMALE GUT	FG	32.40	17.02	12.70
MALE GUT	MG	27.70	6.78	12.90
MEAN GUT	$\bar{G}$	30.10	11.90	12.80

CORRELATION (R)		
FL/ML	MF/MM	FG/MG
.984	.849	.891

TABLE 2 – CORRELATIONS BETWEEN SEXES FOR MANTLE LENGTH, MATURITY AND GUT FULLNESS

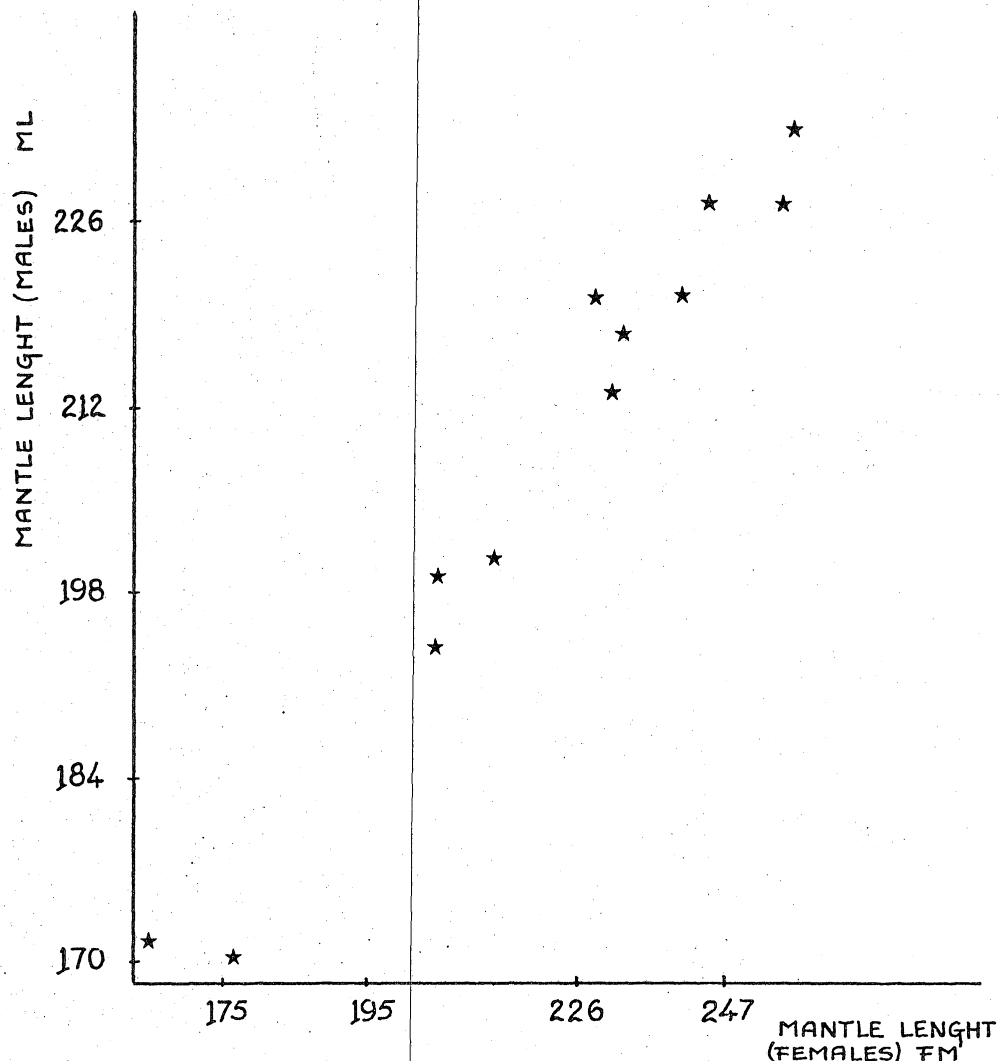


FIG. 1 - REGRESSION OF ML/FL

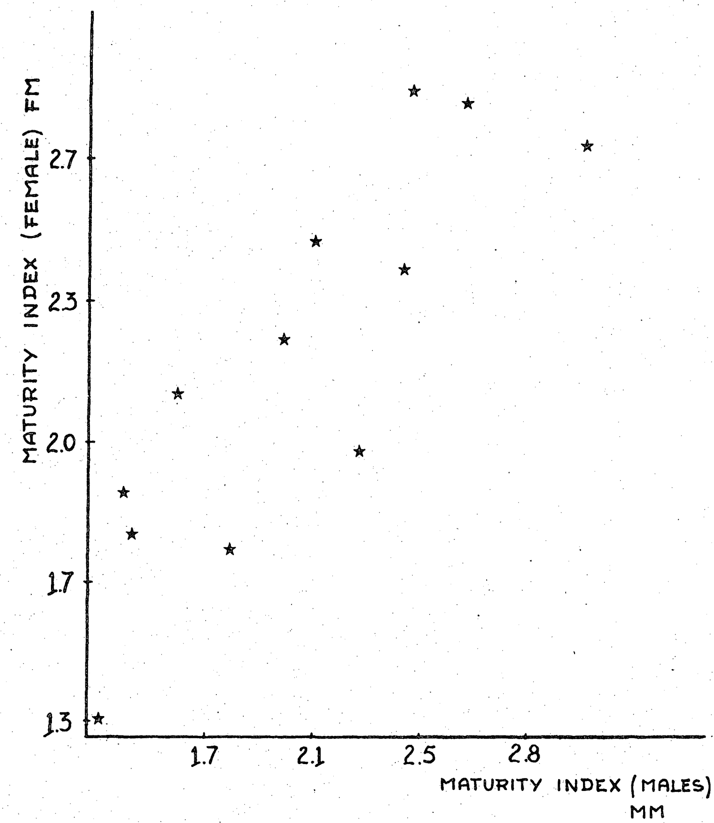


FIG. 2- REGRESSION OF FM ON MM

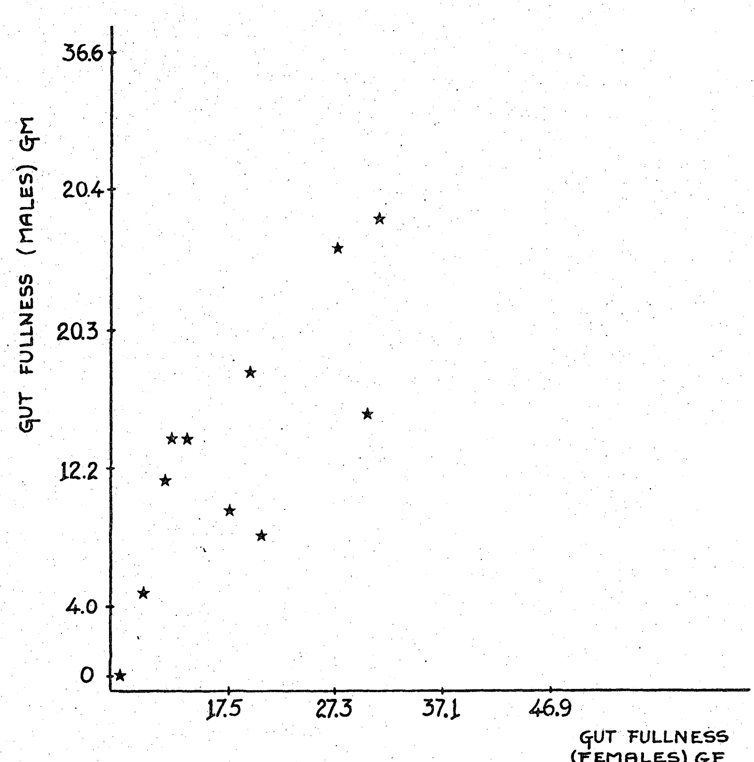


FIG. 3- REGRESSION OF GM ON GF

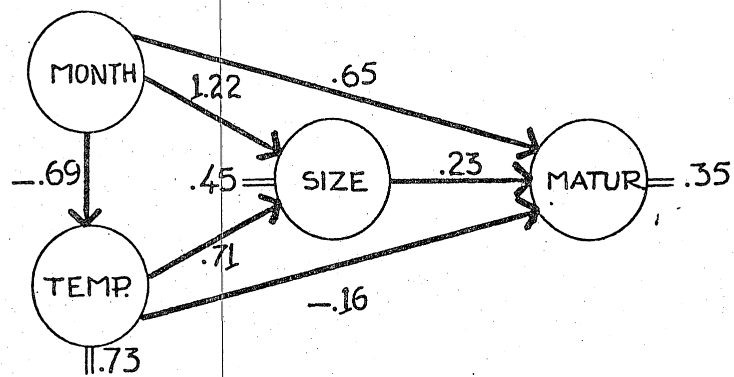


DIAGRAM 1— MATURITY RELATED TO SIZE TEMPERATURE AND MONTH

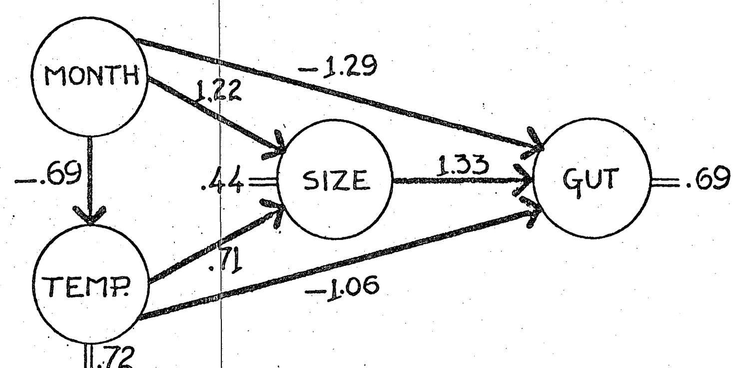


DIAGRAM 2— GUT FULLNESS RELATED TO SIZE TEMPERATURE AND MONTH

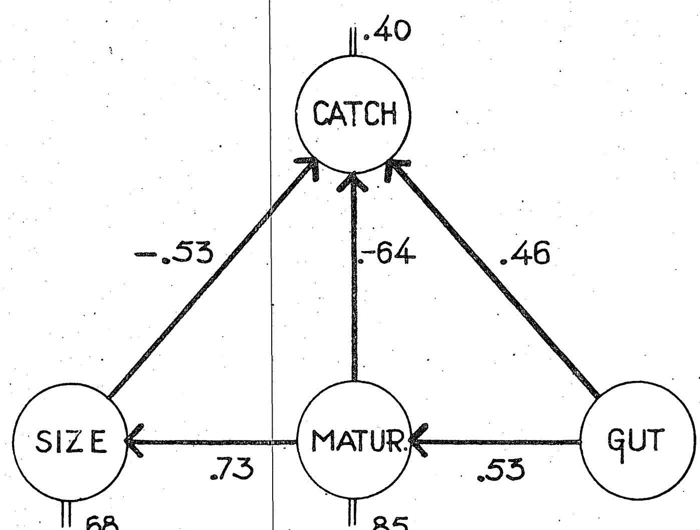


DIAGRAM 3- CATCH RELATED TO SQUID SIZE MATURITY AND GUT FULLNESS

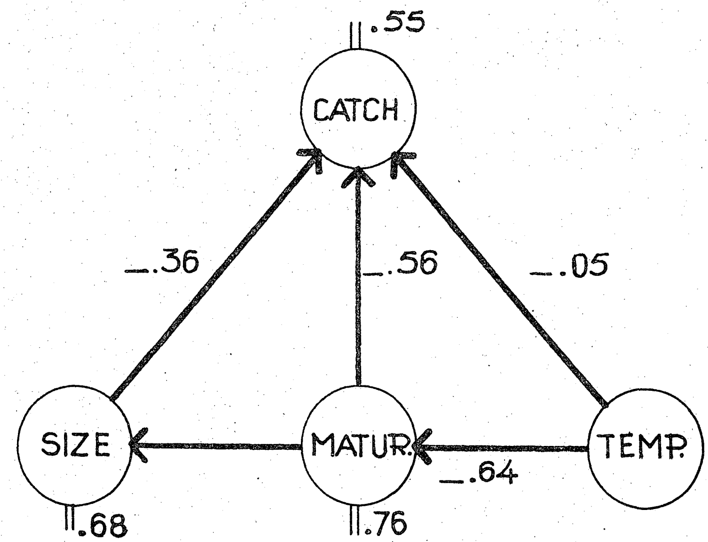


DIAGRAM 4– CATCH RELATED TO SQUID SIZE MATURITY AND WATER TEMPERATURE

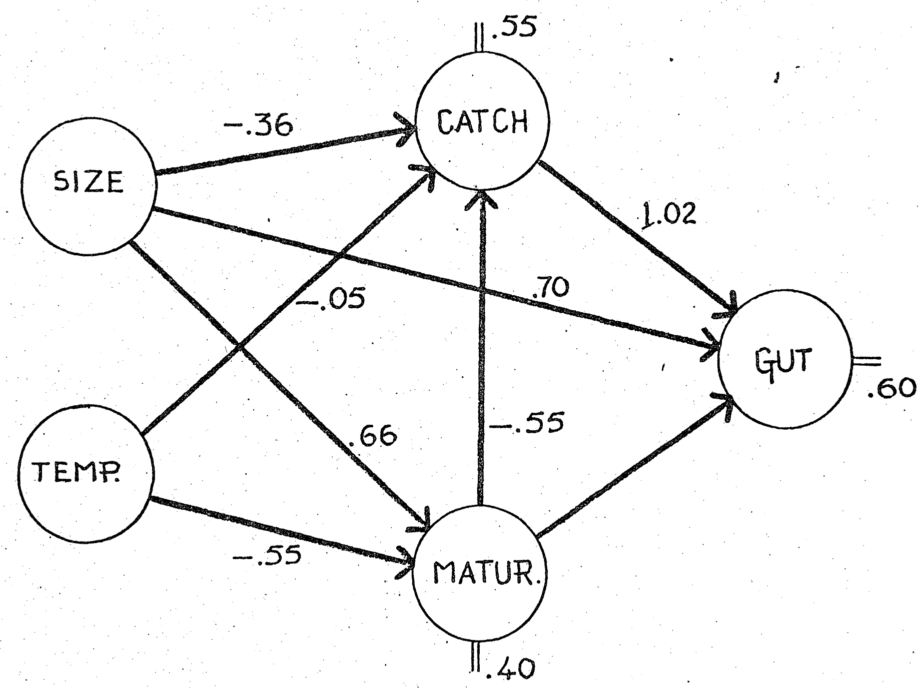
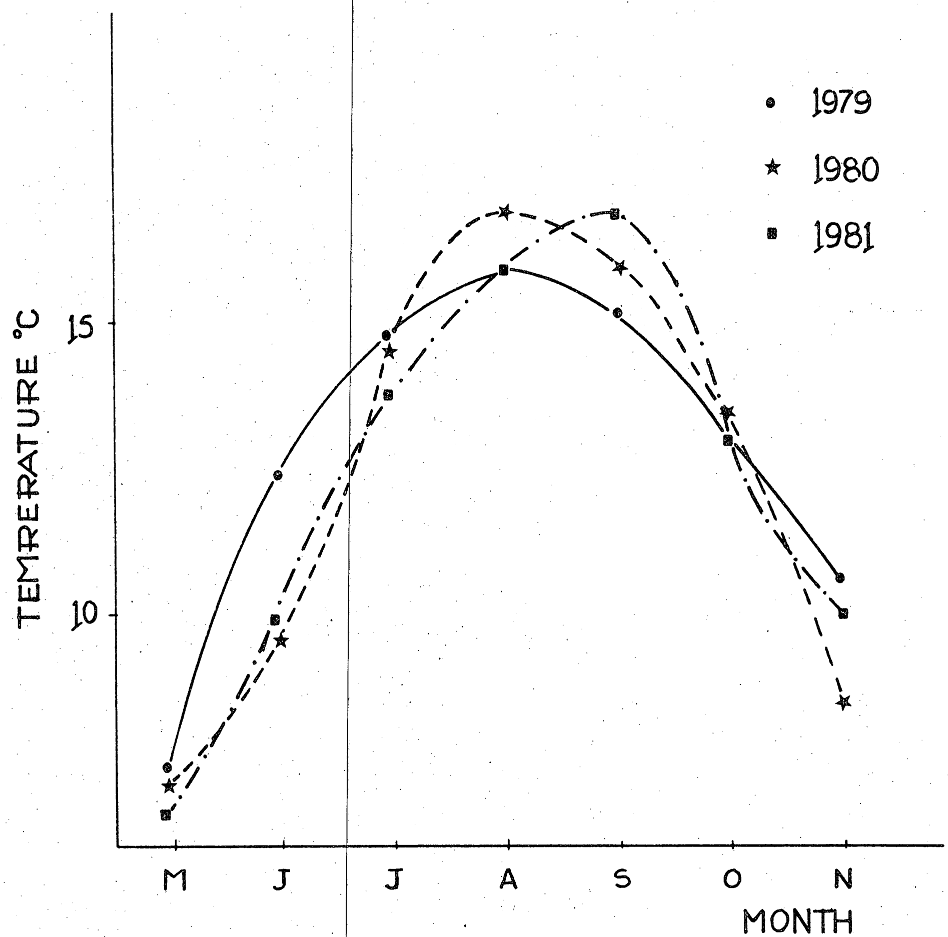


DIAGRAM 5— COMBINED RELATIONSHIPS BETWEEN CATCH, SQUID SIZE, MATURITY, GUT FULLNESS AND WATER TEMPERATURE

APPENDIX I



1- SURFACE WATER TEMPERATURE TRENDS FOR 1979-1981 ON THE SCOTIAN SHELF AREA

APPENDIX II

Correlation matrix for all the analyses used in this study.

	MONTH	TEMP	CATCH	SR	MATURE	SIZE
TEMP	-.69078					
CATCH	-.08616	.35652				
SR	.43790	-.63749	-.32375			
MATURE	.93448	-.64439	-.78714	.46263		
SIZE	.73508	-.13815	-.76084	-.00987	.73394	
GUT	.41295	-.34793	-.15441	-.07573	.52723	.52243

Summary of multiple regression statistics using catch as dependent variable and month, temperature, gut fullness, sex ratio, maturity and size as independent variables.

* * * * * * * * * M U L T I P L E   R E G R E S S I O N * * * * * * * *

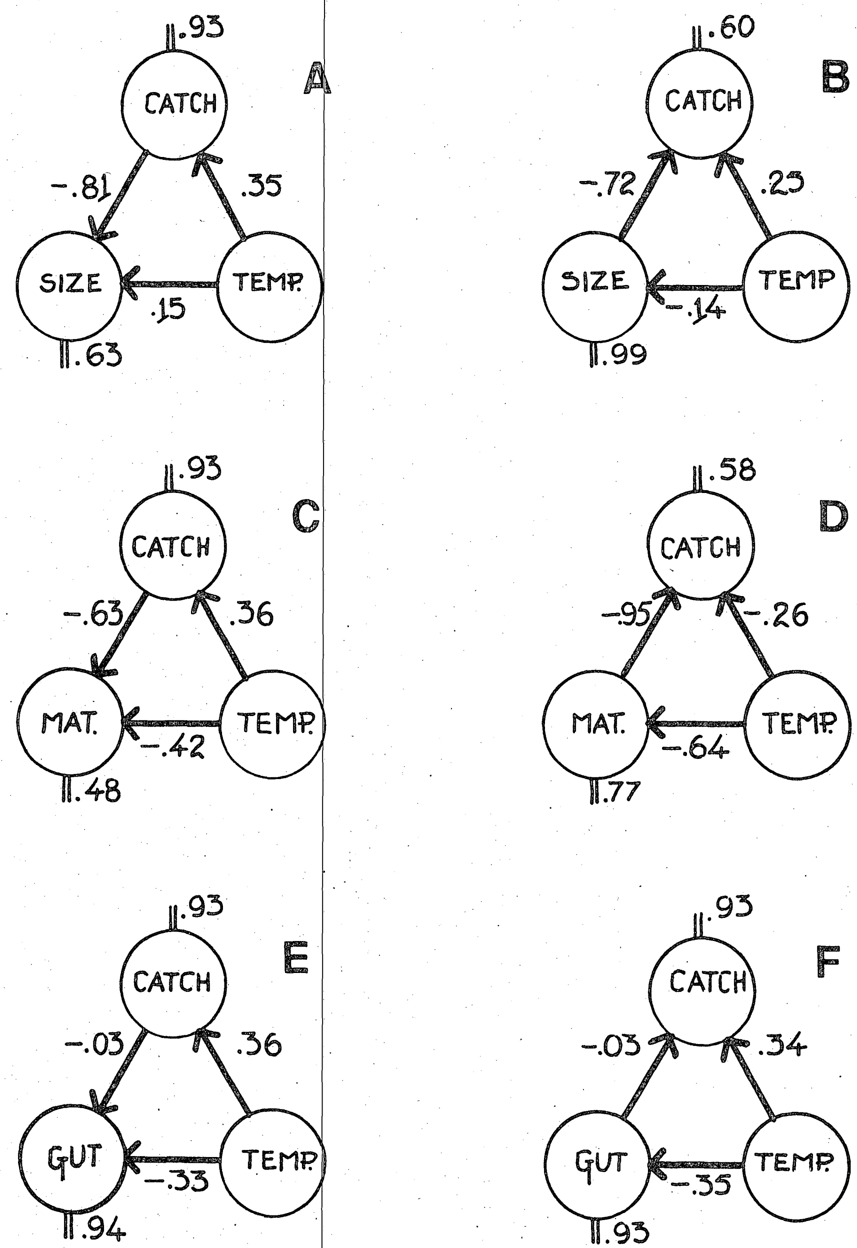
DEP. VAR... CATCH

VARIABLE(S) ENTERED ON STEP 6
SIZE

MULTIPLE R	.9788	ANOVA	DF	SUM SQUARES	MEAN SQ.	F
R SQUARE	.9580	REGRESSION	6.	58.631	9.772	18.986
STD DEV	.7174	RESIDUAL	5.	2.573	.515	SIG. .003
ADJ R SQUARE	.9075	COEFF OF VARIABILITY		10.8PCT		

VARIABLE	B	S.E. B	F	SIG.	BETA	ELASTICITY
MONTH	-2.749	.736	13.957	.013	-1.60694	-3.69501
TEMP	-.376	.237	5.906	.059	-.63448	-1.24067
GUT	.022	.035	.394	.558	.10228	.05984
SR	-.189	.239	.629	.464	-.11822	-.04214
MATURE	1.102	1.615	.466	.525	.22171	.35194
SIZE	.011	.026	.181	.688	.11542	.35375
CONSTANT	34.575	4.606	56.359	.001		

APPENDIX III



DIAGRAMS A TO F — CATCH/SIZE/MATUR/GUT/TEMP. INTERACTION