

Causal Analysis of Some Biological Data for *Illex illecebrosus* from the Scotian Shelf

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Abstract

The method of path analysis is applied to data on the biology of the short-finned squid (*Illex illecebrosus*) from the Scotian Shelf. The variables considered in the analysis are catch, size, maturity, feeding, temperature and month. Four hypothesized causal models of the interrelationships of these variables are presented. Temperature and month are shown to have a direct effect on catch-per-day as a measure of abundance, but they also have indirect effects through their action on the other variables. The method of path analysis provides a framework for explicitly examining hypotheses with respect to available data. More widespread application of the method to fisheries data seems warranted.

Introduction

Concurrent with the increasing importance of the fishery for *Illex illecebrosus* in the Northwest Atlantic during the 1970's were large fluctuations in abundance, as indicated by variation in the nominal catches. These fluctuations cannot be attributed to exploitation pressure as fishing effort on the stock increased, because lightly-exploited squid populations have shown similar patterns of variation in abundance. Squires (1957) analyzed a long time-series (1879-1954) of data on the occurrence of *I. illecebrosus* in inshore Newfoundland waters and concluded that the great variability in the data fundamentally resulted from climatic changes. Cycles in abundance of related species of squid have been described by Sasaki (1929) (cited by Lipinski, 1973) who identified cycles of 4-11 years for *Todarodes pacificus*, and by Wiborg (1972) who reported abundance cycles of 3-5 years for *T. sagittatus* during the 1949-65 period.

The influence of temperature on biological processes in cephalopods, such as growth, maturation, spawning and distribution in various areas with different species, has been reported in many studies (Tinbergen and Verwey, 1945; Richards, 1966; Boletzki *et al.*, 1973; Hamabe *et al.*, 1974; O'Dor *et al.*, 1980, 1982; Fedulov and Froerman, MS 1980). However, correlations of squid abundance with abiotic factors are difficult to interpret, due partly to the difficulty of defining abundance for an animal with complex behavioral and distribution patterns. The abundance parameter usually measured for squid, as for other marine organisms,

is relative abundance, and its estimation from catch and fishing effort data presents problems due to the difficulty of assigning effort to the overall squid catch. Additionally, changes in abundance may be a consequence of variable schooling and migration patterns, due to direct effects of physical events such as winds, currents and temperature conditions, or to indirect processes such as changing productivity and hence the food supply in the area, or to real changes in population size. Despite these limitations, the hypothesis that water temperature influences abundance either directly or indirectly through its influence on different biological processes leads to the need to describe causal relationships between abundance, various biological indicators and temperature.

Research on squid populations in the Northwest Atlantic has provided a wide range of biological data. Growth, maturation, food types and population structure of *I. illecebrosus* have been described (Amaratunga, MS 1980a, MS 1980b; Durward *et al.*, 1979), but the interactions between the various biological factors remain unclear. Such data for the squid population on the Scotian Shelf, including catch-per-unit-effort as an indicator of abundance, have been collected routinely for several years by the Invertebrates and Marine Plants Division of the Canadian Department of Fisheries and Oceans, Halifax, Nova Scotia. In this paper, the analysis involves data for 3 years (1979-81), representing seasons of high, medium and low abundance of squid. Mantle length, maturity stage and feeding (percentage of animals with food in their guts) are considered as biological variables which may be causally

related to abundance during the period when squid are available to the fishery. In addition, the effects of temperature and time (i.e. month of sampling) as general abiotic variables were included in the analysis.

A basic premise of the analysis is that the biological and environmental variables interact and so may affect abundance and each other both directly and indirectly. Path analysis, developed by Wright (1934) and described in detail by Li (1975), is suitable for examining such systems when direct or indirect causal paths may be important. In this paper, the method is used to examine the interactions between and among the biotic and abiotic variables.

Materials and Methods

Biotic and abiotic data

The biological database used in this study was derived from samples which were collected routinely by observers on fishing vessels engaged in the squid fishery on the Scotian Shelf during the 1979-81 seasons. These data were supplemented by samples obtained during research vessel surveys of the area.

For the period from July to November of each year, data were initially grouped on a weekly basis and later aggregated on a monthly basis to obtain mean values of mantle length and maturity stage, and average percentage of guts containing food. Maturity stage of each animal was recorded according to the numerical scale (1-5) described by Durward *et al.* (1979) for females and by Mercer (MS 1973) for males. Because the maturity stages of males and females are on different scales, male maturity must be recognized as being more advanced than that of females in this analysis. Data for males and females were combined after appropriate statistical tests indicated no significant differences between the means ($P > 0.05$).

Catch-per-day-fished was used as the indicator of abundance. These data were derived from logbook records of vessels engaged in the squid fishery and were combined to reflect the mean catch-per-day on a monthly basis for the July-November period. In the absence of subsurface temperature data for all locations on the Scotian Shelf where samples of squid were collected, mean surface temperatures by month for the entire shelf were derived from weekly reports by the Canadian Meteorological Centre, Bedford, Nova Scotia. Table 1 contains a summary of the available data,

TABLE 1. Summary of data used in the application of path analysis to variables relevant to the *I. illecebrosus* fishery on the Scotian Shelf, 1979-81.

Year	Month	Surface temp. (°C)	Catch No./day (10 ³)	Mean mantle length (mm)		Mean maturity		Animals feeding (%)	
				M	F	M	F	M	F
1979	Feb	—	—	192	207	2.9	2.9	0.0	0.0
	Mar	—	—	201	219	2.7	2.9	0.0	0.0
	Apr	—	—	—	—	—	—	—	—
	May	7.3	—	133	138	1.0	1.3	15.7	15.7
	Jun	12.3	36	—	—	—	—	4.2	64.7
	Jul	14.8	142	—	—	—	—	—	—
	Aug	16.0	84	220	229	2.1	1.6	25.5	27.3
	Sep	15.2	57	227	246	2.5	2.1	17.9	19.3
	Oct	13.0	62	233	257	2.9	2.4	26.9	31.2
	Nov	10.6	46	228	256	2.8	2.6	36.6	51.8
1980	Feb	2.0	—	160	167	1.2	—	0.0	0.0
	Mar	2.4	—	—	—	—	—	—	—
	Apr	3.1	—	157	160	1.0	1.5	1.1	0.0
	May	7.0	—	168	172	1.3	1.3	36.8	43.2
	Jun	9.5	—	163	169	1.0	1.2	15.1	20.8
	Jul	14.8	96	170	178	1.3	1.4	9.5	17.2
	Aug	17.0	72	193	209	1.7	1.8	4.5	9.4
	Sep	16.0	53	217	233	2.4	2.4	15.4	30.5
	Oct	13.5	39	220	240	2.3	2.0	0.0	7.7
	Nov	8.5	40	201	215	2.7	3.0	8.5	20.3
	Dec	4.7	—	177	217	1.9	2.4	3.4	7.3
	1981	Apr	—	—	—	—	—	—	—
May		6.5	—	130	133	1.4	1.2	4.5	4.7
Jun		9.7	—	142	148	1.2	1.2	6.3	10.6
Jul		13.8	117	171	165	1.7	1.5	13.7	13.8
Aug		16.0	76	200	206	1.9	1.4	11.3	11.7
Sep		17.0	54	214	230	2.0	2.3	13.7	12.7
Oct		12.0	17	—	—	—	—	—	—
Nov		10.0	12	—	—	—	—	—	—
Dec	7.0	—	—	—	—	—	—	—	

although only the July–November data were used in the analysis.

Summary of statistical methods

Although correlation techniques are useful for examining the relationships between variables, the study of cause and effect relationships implies more than simple correlations. "Cause and effect" is a directional concept and regression coefficients have a direction associated with them. Partial regression coefficients can be used to examine the relationship between two variables by holding the effect of other variables constant. Li (1975) has drawn a useful parallel between partial regression coefficients and partial derivatives to allow consideration of the influence of interacting variables in a hypothesized causal scheme. A path, which connects two variables in a path diagram, may be direct with no intermediate variables or indirect (compound) with several component paths and intermediate variables. The partial regression coefficient associated with each path is called a path coefficient. If the variables in the model are standardized to mean zero and variance one, inferences can be made concerning the relative strength of various pathways to a variable. There are general rules for interpreting such path diagrams:

1. Cause and effect relationships are unidirectional and are shown by arrows with the head of the arrow at the dependent variable. Correlations which imply no causality are shown with double-headed arrows.
2. All hypothesized factors (predictors) which contribute to total variation of the dependent variable(s) are included in the diagram. The residual coefficient which is a composite of unknown sources of variation is indicated by a 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 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 which affect that dependent variable. Alternatively, this value is one minus the square of the residual coefficient.

In contrast to path analysis, multiple regression may be represented by a very simple path diagram with only direct relationships between dependent and independent variables (i.e. with no compound paths). More complicated path models can be thought of as sets of simultaneous multiple regressions. See Nie *et al.* (1975) for calculation procedures, and Li (1975) for a full description of path analysis.

TABLE 2. Correlation matrix for all variables used in this analysis of *I. illecebrosus* data for the Scotian Shelf.

	Month	Temp.	Catch	Maturity	Size
Temperature	-0.69				
Catch	-0.89	0.35			
Maturity	0.93	-0.64	-0.79		
Size	0.73	-0.14	-0.76	0.73	
Feeding	0.41	-0.35	-0.15	0.53	0.52

Results and Discussion

As the initial step in the study, and for comparison with the path analysis to follow, a stepwise multiple regression was performed with catch as the dependent variable and the remaining variables as predictors (Table 2). This analysis indicated that significant proportions of the total variance (F-test, $P < 0.01$) were explained by only two variables (month and temperature). The fitted model is

$$\text{CATCH} = -1.22 (\text{MONTH}) - 0.49 (\text{TEMP})$$

with a coefficient of determination $r^2 = 0.91$.

Several path diagrams of causal relations between the variables were hypothesized. The sample correlation matrix of the variables (Table 2) is useful in examining these diagrams with respect to rule 4 of the preceding section. The ability of a given hypothesis to explain the observed correlations between variables may be analyzed by comparing the coefficients in Table 2 with those calculated from the diagram (see Li (1975) for details). Also, with the use of rule 4, each diagram hypothesizes how particular observed correlations may arise. Examples of this are given below.

In Fig. 1, size is hypothesized to be affected by temperature and month and each of these affects maturity both directly and indirectly. Month and temperature have a strong positive effect on size, but, because of the strong negative path coefficient between month and temperature, there is a compound pathway from month through temperature to size with an overall negative sign. This follows the rule that the coefficient of a compound path is the product of the coefficients of its component paths. Thus, the effect of month on size of squid during their presence on the Scotian Shelf appears to be mediated by the declining surface temperatures observed during the period of study. From Table 2, the sample correlation between temperature and size may be calculated as the sum of the direct path coefficient and the effects of month and maturity, i.e. $0.71 + (0.69 \times 1.22) + (-0.16 \times 0.23) = -0.17$, which is quite close to the sample correlation.

Maturity increases with both month and size, with month having the strongest effect (Fig. 1). Temperature appears to have a slight negative effect. However,

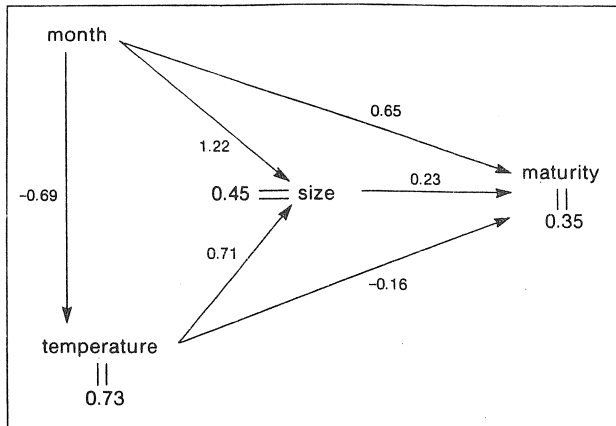


Fig. 1. Path diagram of the interactions between month, temperature, squid size and maturity for *I. illecebrosus* during the fishing season on the Scotian Shelf.

the much stronger effect of temperature through size to maturity has an overall positive sign. The indirect effects of month on maturity are also positive, reflecting the progress of maturation with time. However, the 3-component path from month through temperature and size to maturity ($-0.69 \times 0.71 \times 0.23$) has an overall negative sign, implying that the maturation is balanced by the size of the animal and the environmental conditions. The observed negative correlation between maturity and temperature appears, from the model, to be a result of the direct negative effect of temperature as well as the effects of month on each, both effects having opposite signs.

A similar diagram (Fig. 2) shows the effects of month, temperature and size on feeding. The very strong negative effects of both month and temperature seem to be largely balanced by their positive effects on size and the positive effect of size on the number of animals feeding. The negative correlation between temperature and feeding similarly seems to be balanced by the negative effects of month on both of these variables. The overall impression is that there are probably strong physiological effects of changing temperature and month (and hence photoperiod), but that these effects change with size of the animals. Also, immigration and emigration in the study area may account for some of the variation, because squid gradually depart from the fishing grounds as the season progresses (Amaratunga, MS 1980a).

The two preceding diagrams may be viewed as first stages for more complicated models of variation in catch. Figure 3 extends the hypotheses of Fig. 1 to include catch. The effects of month are all quite strong, as are the effects of temperature with month controlled. Here, temperature seems to have a direct negative effect on catch, whereas the observed correlation between temperature and catch is positive (Table 2).

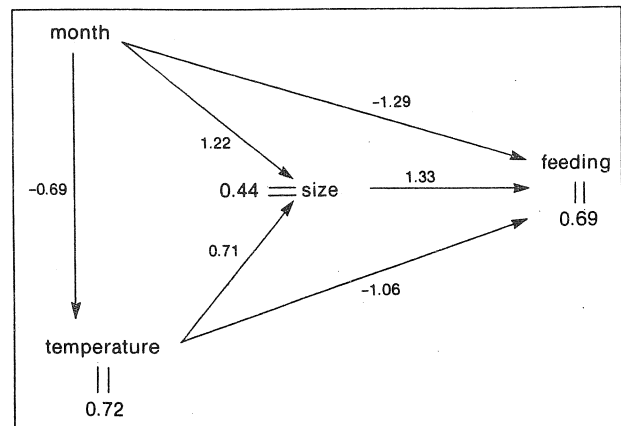


Fig. 2. Path diagram of the interactions between month, temperature, squid size and feeding for *I. illecebrosus* during the fishing season on the Scotian Shelf.

From the path diagram (Fig. 3), it is clear that this is due to the negative effects of month on both temperature and catch, producing a positive association between the two variables. The compound path from temperature through size to catch also has a positive effect. Considering only the biotic variables, it appears that catch responds more to size of squid available to the fishery than to their maturity state. However, both size and maturity have small positive effects on catch, possibly reflecting the migratory patterns of animals as they grow, become mature and vary in their availability to the fishery.

Figure 4 is an extension of the paths shown in Fig. 2. The direct effect of feeding on catch is quite small, and, while the direct effect of size on catch is also small, its effect on catch through feeding is quite large. Similarly, there is a pathway from temperature through feeding to catch that accounts for part of the negative effect of temperature on catch. Again, the relationships between these variables are probably affected by the migration patterns of the animals in relation to feeding and maturation.

Conclusions

This analysis involves a technique for examining the interactions among variables in more detail than the methods of correlation and multiple regression commonly used in fisheries biology studies. It is important to note that path analysis is not a method of testing hypotheses, although goodness-of-fit measures are possible, but rather for examining the consequences of specific hypotheses about the causal structure of a set of variables with respect to the available data. In other words, when certain hypotheses are given about the interactions of a set of variables, path analysis is useful to examine the relative strengths of different paths

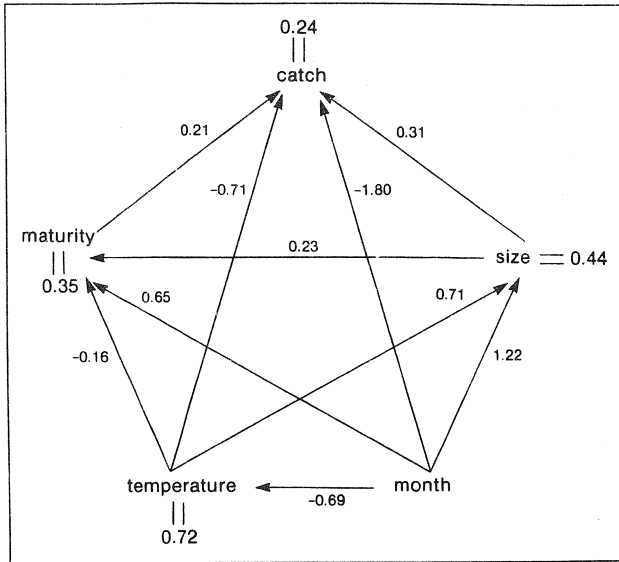


Fig. 3. Path diagram extending the parameters in Fig. 1 to include catch (number per day) for *I. illecebrosus* during the fishing season on the Scotian Shelf.

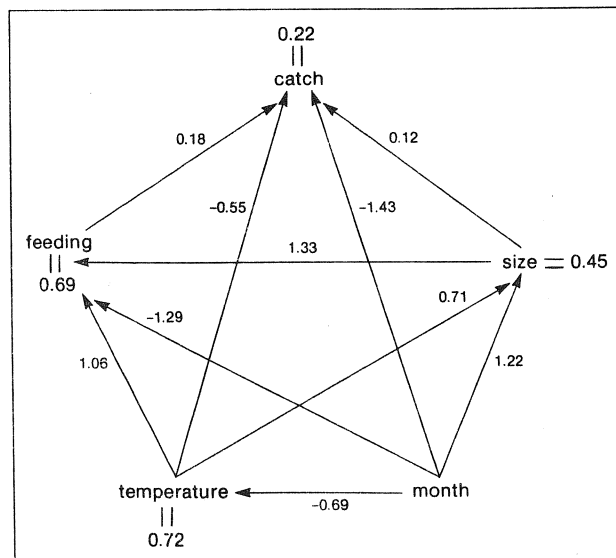


Fig. 4. Path diagram extending the parameters of Fig. 2 to include catch (number per day) for *I. illecebrosus* during the fishing season on the Scotian Shelf.

required to closely represent the observed patterns in the data.

The data used in this analysis have several drawbacks. The index of temperature could possibly be improved upon by using cumulative values rather than monthly means, and a better index of abundance than catch-per-day could be developed. Nevertheless, the models presented in this study do result in interpretable patterns which provide some insight into the causes of variation in catch (and less clearly in abundance) relative to the types of data that are available.

The results are in substantial agreement with other studies of the biology of *I. illecebrosus* and other cephalopods.

The method of path analysis should be viewed as an interactive process. Many different path diagrams may be analyzed as hypotheses develop. Only four of many representations of the variables are presented in this paper, and the analysis indicated that feedback relationships between catch (abundance) and the biotic variables may be present. Such feedback relationships (Li, 1975) require additional and more refined data and involve more complicated statistical methods.

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