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Empirical Relationships between Phytoplankton & Zooplankton Biomass in Indian Ocean

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Empirical models based on regression analysis are derived using published values of phytoplankton and crustacean zooplankton biomass from Indian Ocean. Three regression models are derived. There is significant correlation between zooplankton and temperature, zooplankton and phytoplankton, zooplankton and PO_4-P and phytoplankton and PO_4-P. Linear regression model is found to be significant at 1% level of significance. Since zooplankton and phytoplankton are significantly positively correlated, zooplankton biomass can be predicted from the phytoplankton biomass using this model. Using multiple regression model it is found that at lower and medium levels, temperature is the prominent factor and at higher level it being PO_4-P followed by phytoplankton, at all levels of concentration of phytoplankton. At the higher level of phytoplankton production ecological efficiency reaches its asymptotic value and almost remains a constant for further increase of phytoplankton.

Theories based on empirical relationships between phytoplankton and zooplankton are becoming increasingly important. Empirical relationships based on regression analysis are derived in this study employing published data on phytoplankton and crustacean zooplankton biomass collected during International Indian Ocean Expedition (IIOE).

These empirical relationships are used to test the Null hypotheses, namely 1) to test H_0:zooplankton biomass is positively linearly related to phytoplankton and hence can be predicted from the latter against the alternate H_1: the relation is not linear and positive; (2) to test H_0: zooplankton biomass can be predicted to a greater confidential level from phytoplankton biomass at constant levels of the parameters like temperature, salinity, oxygen, PO_4-P, NO_3-N and NO_2-N against the alternate H_1: prediction ability cannot be enhanced by the addition of the above parameters and (3) to test H_0: ecological efficiency i.e. ratio of zooplankton to phytoplankton biomass, decreases across the set of 3 levels and the whole set in the regions examined against the alternate H_1: ecological efficiency increases across the set of 3 levels and the whole set.

Materials and Methods

The published data[1] are from *R V Anton Bruun* cruises 1 (12 March to 10 May 1963), 4A (25 Sept. to 8 Nov. 1963) and 7 (29 July to 10 Sept. 1964). These data collected from 103 stations were divided into 3 levels based on phytoplankton production (Table 1) expressed as g $C.m^{-2}d^{-1}$.

The phytoplankton in the study area is expressed[2] as cell volume ($\mu g.l^{-1}$) using the constant ratio of chl *a* to cell volume as 0.01. The crustacean zooplankton[3] biomass is expressed as displacement volume (ml. m^{-2}) and the parameters like temperature, salinity, oxygen, PO_4-P, NO_3-N and NO_2-N and chl *a* averaged up to the depth of nearly 100 m (thermocline) are used.

Null hypothesis 1 is tested using linear regression of zooplankton on phytoplankton biomass expressed as log values for each level and overall.

In the linear regression equation,

$$Y_i = a + bX_i$$

Y_i is log zooplankton biomass in the i^{th} station, X_i is log phytoplankton biomass in the i^{th} station; and a, b are regression coefficients obtained using the principle of least squares. This regression equation is tested for significance using ANOVA technique[4] and variability explained by the regression model is calculated. Standard error (S_e) of b^* is calculated from:

Table 1—Different Levels of Stations Based on Phytoplankton Production (dry wt) from the Regions Covered

Region (stations)	Phytoplankton production (g $C.m^{-2}.d^{-1}$)		
	$\leqslant 0.1$	0.11 to 0.25	$\geqslant 0.26$
A (72)	27	37	8
B (27)	1	5	21
C (4)	—	—	4

A = Central Bay of Bengal (lat. 7°27′ to 20°35′N; long. 80°44′ to 97°59′E)

B = Agulhas Current region (lat. 22°34′ to 35°44′S; long. 32°06′ to 43°37′E)

C = Saudi Arabian Coast (lat. 18°31′ to 20°44′N; long. 62° to 64°34′E)

$$S^2_{eb^*} = \frac{\Sigma_i[Y_i - \bar{Y}]^2[1-r^2]}{\Sigma_i[X_i - \bar{X}]^2[N-2]}$$

b^* is tested for its significant departure from 1 using[5] the test statistic $t = \frac{|b^*-1|}{S_{eb^*}}$ with $(N-2)$ degrees of freedom.

To test the second Null hypothesis, a multiple regression model of zooplankton on phytoplankton, temperature, salinity, dissolved oxygen, PO_4-P, NO_3-N and NO_2-N is fitted for log values separately for the 3 levels.

Multiple regression model is

$$Y_i = a_0 + a_1X_{1i} + a_2X_{2i} + a_3X_{3i} + a_4X_{4i} + a_5X_{5i} + a_6X_{6i} + a_7X_{7i}$$

Where Y_i is log zooplankton; X_{1i} to X_{7i} are the log values of phytoplankton, temperature, salinity, dissolved oxygen, PO_4-P, NO_3-N, NO_2-N respectively in the i^{th} station. The constants a_0 to a_7 are multiple regression coefficients calculated using inversion of 8 $\times$ 8 matrix of 8 normal equations. The fitted model is tested for its significance using the ANOVA technique[4]. The variability explained by this model (multiple correlation coefficient R^2) and the relative importance of the parameters are calculated as relative importance of k^{th} parameter =

$$|a_k| \sqrt{\frac{\Sigma_i[Y_i - \bar{Y}]^2}{\Sigma_i[X_{ki} - \bar{X}_k]^2}}$$

$k = 1,2,3,4,5,6,7$

To test the third Null hypothesis a functional regression is fitted for the 3 levels and overall[5] based on log values. The functional regression equation is

$$Y_i = u + b^1X_i$$

where Y_i is log zooplankton and X_i is log phytoplankton in the i^{th} station; u and b^1 are functional regression coefficients and estimated using the method of least product.

Estimate of $b^1 = b^{1*} =$

$$+ \sqrt{\frac{\Sigma_i[Y_i - \bar{Y}]^2}{\Sigma_i[X_i - \bar{X}]^2}}$$ and

estimate of $u = u^* = \bar{Y} - b^{1*}\bar{X}$. This equation is also tested for its significance using ANOVA technique. The variability explained by the model, S_e of b^{1*} and its test of significance for the departure from 1 using the test statistic $t = \frac{|b^{1*}-1|}{S_{eb^{1*}}}$ where $S^2_{eb^{1*}} = S^2_{eb^*}$, t is a Student's statistic with (N-2) degrees of freedom.

Results and Discussion

Table 2 gives the analysis of covariance for testing the equality of the slopes of the linear regression lines of the 3 regions. The slopes of the lines are not significantly different at 1 % level suggesting identical relationship between the abundance of zooplankton and phytoplankton in all the 3 regions. The regions are therefore combined together to group the data into 3 levels, based on phytoplankton production for further analysis. Table 3 gives the mean and standard deviation (%) of all variables under study. NO_2-N is least consistent while salinity is most consistent. Table 4 gives the correlation coefficients of all variables. From this table, zooplankton is significantly positively correlated with phytoplankton. Phytoplankton is highly correlated with PO_4-P at all levels and with dissolved oxygen only at higher level. But zooplankton is highly correlated with PO_4-P and temperature at all levels.

The linear regression equations are

$Y_i = 0.9386 + 0.2165\ X_i$ for level 1
$Y_i = 0.6179 + 0.6231\ X_i$ for level 2
$Y_i = -0.3959 + 1.2071\ X_i$ for level 3
$Y_i = 1.6971 + 0.4712\ X_i$ for the overall.

All these equations are significant at 1 % level, i.e., at all levels of phytoplankton, the regression equations can predict a significant part of zooplankton from the phytoplankton biomass. From Table 5 the variability explained is found to be >50 % only at 2nd level and it is the least at level 1. Since variability explained is <50 % in most cases and in addition to justify the above conclusion about the nature of relationship at higher concentrations, a multiple regression model with the additional parameters, temperature, salinity, oxygen, PO_4-P, NO_3-N and NO_2-N is fitted. The fitted equations are

For level 1:

$$Y_i = 6.4544 + 0.2430\ X_{1i} - 4.0101X_{2i} + 0.1759\ X_{3i} - 0.0757\ X_{4i} - 0.0401\ X_{5i} + 0.0054\ X_{6i} + 0.1919\ X_{7i}$$

For level 2:

$$Y_i = -21.9735 + 0.5375\ X_{1i} - 15.9009\ X_{2i} + 0.4867\ X_{3i} - 0.9973\ X_{4i} - 0.8646\ X_{5i} + 0.0452\ X_{6i} + 0.0066\ X_{7i}$$

For level 3:

$$Y_i = -0.9303 + 3.3755\,X_{1i} + 4.1976\,X_{2i} + 0.4692\,X_{3i} + 1.4787\,X_{4i} - 6.3299\,X_{5i} - 0.4486\,X_{6i} + 3.4240\,X_{7i}$$

These regression equations are found to be significant at 10% level at level 1 and at 1% level at levels 2 and 3. Multiple regression equations can predict zooplankton from phytoplankton along with other parameters. Also we can estimate zooplankton

Table 2—Analysis of Covariance Table for Comparison of Slopes of Regression Lines

Source	df	Σx^2	Σxy	Σy^2	Reg. coef.	Deviations from regression		
						df	SS	MS
Within Bay of Bengal	71	8.1043	3.5869	8.3281	1.2213	70	3.9475	0.0564
Within Agulhas	26	2.7321	0.4637	1.4759	0.8142	25	1.0984	0.0439
						95	5.0459	0.1003
Pooled within	97	10.8364	4.0506	9.8040	1.0613	96	5.5051	0.0573
		Difference	between slopes			1	0.4592	0.4592

Comparison of slopes F = 4.5768 (df = 1,97) NS

There is no significant difference between the slopes of regression lines of Bay of Bengal and Agulhas Current region.

Regression line for Bay of Bengal is $Y = -0.0926 + 1.2212X$

Slope = 50.687°

Regression line for Agulhas Current region is $Y = 0.0509 + 0.8142X$

Slope = 39.15°

Regression line for Saudi Arabian coast is $Y = -0.1769 + 1.0921X$

Slope = 47.52°

Since slope of regression line of Saudi Arabian coast is between those of Bay of Bengal and Agulhas region, there is no significant difference between the slopes of the 3 regression lines

Table 3—Mean and SD of Various Characters under Study at Different Levels

[Percent SD values are given in parentheses]

Character	1	2	3	Over all
Phytoplankton	0.7900 (41.04)	1.0100 (49.09)	1.3300 (12.02)	1.0600 (40.41)
Zooplankton	1.1100 (15.11)	1.2500 (32.28)	1.2100 (30.91)	1.2000 (29.14)
Temperature	1.4430 (1.64)	1.4350 (2.43)	1.3490 (8.51)	1.4010 (5.80)
Salinity	1.5380 (5.87)	1.5400 (0.81)	1.5520 (7.69)	1.5440 (5.42)
Oxygen	0.6960 (8.99)	0.6950 (13.76)	0.7480 (15.37)	0.7140 (13.73)
PO_4-P	0.1318 (51.75)	0.1314 (105.25)	0.1308 (70.26)	0.1313 (82.64)
NO_3-N	0.5200 (53.92)	0.6100 (67.17)	0.4700 (76.19)	0.5400 (67.73)
NO_2-N	0.1700 (169.80)	0.1000 (141.18)	0.0600 (111.32)	0.1100 (180.04)

Table 4—Various Correlation Coefficients Between Phytoplankton, Zooplankton and Other Characters and Their Test of Significance

Level	Character	Phytoplankton	Zooplankton	Temperature	Salinity	Oxygen	PO_4-P	NO_3-N	NO_2-N
1	Phyto:	1.00	0.42†	NS	NS	NS	0.42†	NS	NS
	Zoopl:	0.42†	1.00	−0.42†	NS	NS	0.40†	−0.43†	NS
2	Phyto:	1.00	0.77‡	NS	NS	0.96‡	0.89‡	NS	NS
	Zoopl:	0.77‡	1.00	−0.79‡	0.36‡	NS	0.68‡	NS	NS
3	Phyto:	1.00	0.58‡	NS	NS	0.97‡	0.97‡	NS	0.91‡
	Zoopl:	0.58‡	1.00	−0.39†	NS	NS	0.51‡	NS	NS
Overall	Phyto:	1.00	0.58‡	−0.25‡	0.27	0.54‡	0.70‡	NS	0.63‡
	Zoopl:	0.58‡	1.00	NS	0.28‡	NS	0.49‡	NS	NS

Level of significance P = † < 0.05; ‡ < 0.01

Table 5—Regression Coefficient b of Zooplankton on Phytoplankton, SE of b, Test Statistic t and Variability Explained by Linear Regression Model

Level	b^*	SE (b^*)	t statistic (df)	Variability explained (%)
1	0.2165	0.0918	8.53† (26)	14.5
2	0.6231	0.0827	4.55† (40)	58.1
3	1.2071	0.3599	0.58 (31)	31.1
Overall	0.4712	0.0667	7.93† (101)	33.7

†Level of significance P = <0.01

for various levels of phytoplankton keeping the other parameters at constant levels. From Table 6 variability explained is found to be comparatively more than that explained by the linear regression model at all levels. By including more parameters explained variability within the distribution of zooplankton at various levels of distribution of phytoplankton can be increased. Hence we can accept the 2nd Null hypothesis at 10% level at the least. From Table 6 the relative importance of the parameters included in the multiple regression model is as follows:

For level 1:

Temperature > phytoplankton > NO_3-N > salinity > oxygen > PO_4-P > NO_2-N

For level 2:

Temperature > phytoplankton > PO_4-P > oxygen > NO_2-N > Salinity > NO_3-N

For level 3:

PO_4-P > Phytoplankton > temperature > NO_3-N > oxygen > NO_2-N > salinity

Temperature is the most prominent factor at lower levels and PO_4-P at higher level followed by phytoplankton at all levels. It is seen that relative importance of PO_4-P increases with increase in phytoplankton finally occupying the first place at higher level. Relative importance of salinity decreases, of oxygen almost remains the same and that of nitrogen group does not vary much with increase of phytoplankton.

From Table 5, regression coefficient, b^*, is significantly different from 1 at lower levels and for the whole set which suggests a curvilinear relationship between zooplankton and phytoplankton at lower levels of concentration of phytoplankton. But at higher level the regression coefficient is not significantly different from 1 which suggests a linear relationship at

Table 6—Percentage of Variability Explained by Multiple Regression Model and Relative Importance of Parameters Used

	Level		
	1	2	3
Variability explained (%)	21.8	57.1	46.0
Relative importance			
Phytoplankton (a_1)	0.47	0.66	1.44
Temperature (a_2)	0.56	1.37	1.29
Salinity (a_3)	0.09	0.01	0.15
Oxygen (a_4)	0.03	0.24	0.45
PO_4-P (a_5)	0.02	0.30	1.57
NO_3-N (a_6)	0.01	0.05	0.43
NO_2-N (a_7)	0.33	0.00	0.69

higher level. To study the nature of the change of the ratio of zooplankton to phytoplankton with respect to phytoplankton, the functional regression model of zooplankton on phytoplankton is fitted. The fitted model is

$$Y_i = 0.7015 + 0.5158\ X_i \text{ at level 1}$$
$$Y_i = 0.4281 + 0.8101\ X_i \text{ at level 2}$$
$$Y_i = -1.9032 + 2.3394\ X_i \text{ at level 3}$$
$$Y_i = 0.3345 + 0.8195\ X_i \text{ overall.}$$

All functional regression equations are significant at 1% level and hence can explain a significant part of the variability inherent in the prediction equation. From Table 7, Model 3 can explain 50% variability in almost all cases. At level 2 it being the maximum. From Table 7, standard error of b^{1*} is more at higher level and b^{1*} is significantly different from 1 at 5% level in all cases. This shows that a curvilinear functional relationship is suitable. Again b^{1*} increases with increase in phytoplankton. But $b^{1*} > 1$ and intercept > 0 at lower levels and over all. Since (i) a curvilinear relationship is found to be suitable for the relationship of zooplankton on phytoplankton and $b^* < 1$ in model 1 and it increases with increase in phytoplankton and rate of increase is less than that of phytoplankton, and (ii) at lower levels, the functional regression is also found to be curvilinear and $b^{1*} < 1$ and intercept > 0 and b^{1*} increases with increase in phytoplankton, the ratio of zooplankton to phytoplankton i.e., ecological efficiency decreases with increase in phytoplankton. But the rate of decrease of ecological efficiency is more than that of increase of phytoplankton at lower levels. Since a linear relationship is found to be appropriate for the relation of zooplankton on phytoplankton at the higher level and $b^* > 1$ and intercept < 0, zooplankton increases with increase in phytoplankton and rate of increase is not very much significantly different from the rate of increase in phytoplankton.

Table 7—Functional Regression Coefficient b^1*, SE (b^1*), Test Statistic t 95% and 99% Confidence Interval (CI) for b^1 and Variability Explained by Functional Regression Model

	Level			Overall
	1	2	3	
b^1*	0.5158	0.8101	2.3394	0.8195
SE (b^1*)	0.0918	0.0827	0.3599	0.0667
Test statistic t	5.2700†	2.3000†	3.7200†	2.7100†
95% CI for b^1	0.5158 ± 0.1888	0.8101 ± 0.1654	2.3394 ± 0.7349	0.8195 ± 0.1322
99% CI for b^1	0.5158 ± 0.2552	0.8101 ± 0.2244	2.3394 ± 0.9898	0.8195 ± 0.1751
Variability explained (%)	39.7	76.9	50.0	57.1

†Level of significance $P = < 0.05$

Again a curvilinear functional regression is found to be suitable and $b^1 * > 1$ and intercept < 0, ecological efficiency increases with increase of phytoplankton. But the rate of increase of ecological efficiency has no significant relation to the rate of increase of phytoplankton at this high level. This is because the higher level considered, consists of that volume of phytoplankton which is $= 1\ \mu g\ l^{-1}$ and above. This same range of volume is found to occur at the lower levels, of concentration where it is found that ecological efficiency has almost reached its assymptotic value and thereafter it remains almost a constant for further increase of phytoplankton in that range of volume. Therefore at higher level of concentration, actually ecological efficiency decreases with increase in phytoplankton. This level being the assymptotic part of the first two levels, we get all points plotted being scattered even though not so widely. This change in the relationship at the higher level can be attributed to high abundance of phytoplankton, which is not a limited factor whereas consumption of phytoplankton by zooplankton is a limited factor.

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