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Kalle REMM

A STATISTICAL METHOD FOR THE ASSESSMENT OF ECOLOGICAL RELATIONSHIPS ON THE EXAMPLE OF *FILINIA LONGISETA* (EHR.) (ROTATORIA)

Presenting the relationship between the success of a species and an environmental gradient is discussed. A procedure of calculating the relationship curve from scattered data based on the moving average method is described and exemplified on the abundance data of the zooplankton species *F. longiseta* from the Matsalu Bay (western coast of Estonia). Statistically significant relationships were found between the logarithmic abundance of *F. longiseta* and season, water salinity, chlorophyll *a* concentration, water temperature, and pH.

Introduction

A considerable part of ecological studies deals with the assessment of relationships between certain biological and environmental data. Usually, the aim is to find the ecological optima and tolerance limits for a species or to prognosticate the values of certain ecological variables under certain conditions. Various statistical and graphical techniques have been used, such as linear and nonlinear, simple and multiple regression analysis, classification and ordination methods, histograms and empirical curves, delimitation of the area or space in the hypervolume of environmental factors, and scatter diagrams.

It is generally known that species have optima on environmental gradients and we should not expect the relationship between environmental variables and the success of a species (abundance, productivity or any other measure) to be linear or even monotonic, as has been strongly stressed by R. H. Green and G. L. Vascotto (1978). In natural communities the ecological optimum is presumably influenced by the pressure from other species through competition, predation, and parasitism. Thus, in some cases even more than one optimum is possible under natural conditions. The spatial structure of the environment may also affect the abundance distribution of a species on environmental gradients (Malanson, 1985). This makes the mathematical presentation of the ecological relationship curve quite a complicated problem. Linear models are reliable only within a limited range of environmental gradients. The same holds true for other standard functions which do not reflect causal relations between original data. For example, the square function is sometimes used in the regression analysis of ecological data (Hart, Latta, 1986; Lasn, 1978; Мартин, Ээнсаар, 1983). However, these equations reflect the real relationship only within the range of the author's data used for the calculation of regression equations. As a rule, the limits of ecological reliability are not presented for regression formulas (e. g. Johansson, 1983; Madhupratap et al., 1977; McCanley, Kalfi, 1981; Shastri, George, 1977; Коен, 1977; Милиус et al., 1986; Тимохина, 1986; Трофимова et al., 1986).

Another possible approach is to derive empirical functions between the variables under consideration without predetermining any formal model. Usually such empirical functions are inconvenient to present in

the short formal way of equations, but at least in some cases it would be preferable to do without a simple formula than to have formulas with no ecological meaning. A procedure of constructing empirical functions between two variables is described below.

Material

Data on the abundance of the rotifer species *Filinia longiseta* (Ehr.) from 187 zooplankton samples collected from May to September (incl.) in the years 1977—1986 from the Matsalu Bay, western coast of Estonia, were analysed. All zooplankton samples were collected with a 10 l bucket from the surface layer of water. In most cases 100 l of water were filtered through a plankton net of 90 μm mesh size. When the seston content of the water was very high, only 10—50 l were filtered. Samples were preserved in 2—4% formalin before examination. The water temperature and depth were measured, and a sample of water was collected to measure salinity, pH, and chlorophyll *a* concentration. However, not all of these environmental factors were measured on each sampling occasion (the Table).

F. longiseta abundance and chlorophyll *a* concentration were log transformed because the growth rates of plankton species were expected to be approximately exponential, and in order to normalize the highly asymmetrical distribution of abundance and chlorophyll data. Formula (1) was used as suggested by several authors (Elliott, 1977; Lewis, Taylor, 1967; Southwood, 1966)

$$N_i = \log_{10}(n_i + 1), \quad (1)$$

where n_i — abundance of *F. longiseta* (ind./m³) or chlorophyll *a* concentration ($\mu\text{g/l}$), N_i — transformed abundance or chlorophyll *a* concentration, i — index of a sample. Only transformed data (N_i) were used in calculations and, thus, all means reported in the following parts of this paper are, in essence, the geometric means of the original data. The overall frequency of occurrence of *F. longiseta* was 42.8% and the overall mean abundance was 1.161 which, according to the transformation, equals 13.5 ind./m³.

Methods

Suppose we have an environmental factor X , a biological (functional) variable Y , and a set of measurements of X and Y denoted by X_i and Y_i , and we wish to extract the general relationship from the scattered data. We can consider the relationship of interest as the trend (and the cyclical component) of the classical time series analysis (see, e. g. Anderson et al., 1981). One should not expect the trend component of time series to follow each up-and-down movement, rather it reflects the gradual shifting. In a similar way we are going to extract a generalized relationship from the ecological data set.

A well-known method for smoothing out fluctuations in time series is the moving average method. In order to apply this method we have to divide the X -axis (analogous to the time-axis) into parts or steps and calculate the average Y_i (\bar{Y}_j) at every step (j — index of step). As \bar{Y}_j corresponds actually only to the middle point (MX_j) of every averaging area ($MX_j \pm E$), it is desirable to make steps as frequent as possible. However, the narrower the extent of averaging (E), the more occasional fluctuations are in the moving average. It is possible to overcome this dilemma by making E independent of the length of step intervals (S). So S can have a reasonable minimum value and at the same time E can

be given an optimal value according to the purpose of the study and the set of data. The trial and error approach can be used for selecting a suitable value for E . In brief, the moving average is calculated from the overlapping areas of the environmental gradient and the curve of ecological optimum is plotted as a broken line through all \bar{Y}_j . An analogous approach is described in general terms also by W. S. Cleveland and R. McGill (1985).

To obtain more reliable relationships and to avoid undesirable edge effects, it is useful to differentiate the relative contribution of Y_i to \bar{Y}_j (the moving average at a point MX_j) according to the distance between X_i and MX_j . The smaller $|MX_j - X_i|$, the higher the reliability of the contribution of Y_i to \bar{Y}_j . In order to differentiate the relative importance of Y_i , a corrective coefficient (Q_{ij}) was calculated in this contribution according to the formula

$$Q_{ij} = 1 - (MX_j - X_i)^2 / E^2 \quad (2)$$

and the weighted means

$$\bar{Y}_j = \frac{\sum_i (Q_{ij} Y_i)}{\sum_i Q_{ij}} \quad (3)$$

Q_{ij} was also used in the calculations of the confidence interval ($\bar{Y}_j \pm T_j$) for each Y_j according to the ordinary t -test

$$T_j = t \sqrt{\frac{\sum_i (Q_{ij} (\bar{Y}_j - Y_i)^2)}{\sum_i Q_{ij} (\sum_i Q_{ij} - 1)}} \quad (4)$$

where T_j — the confidence limit, t — the value of Student's t -distribution corresponding to $\alpha = 0.05$ and $\sum_i Q_{ij} - 1$ degrees of freedom.

To evaluate and compare the empirical curves obtained by this method the correlation index R and F -ratio were used.

$$R = \sqrt{1 - \frac{\sum_i (\hat{Y}_i - Y_i)^2}{\sum_i (\bar{Y} - Y_i)^2}} \quad (5)$$

$$F = \frac{\sum_i ((\bar{Y} - Y_i)^2 - \sum_i (\hat{Y}_i - Y_i)^2) (n - 1)}{\sum_i (\hat{Y}_i - Y_i)^2 (k - 1)} \quad (6)$$

$$k = \frac{X_{\max} - X_{\min}}{E} + 1 \quad (7)$$

where $k - 1$ and $n - k$ are the degrees of freedom for F , \bar{Y} — mean of all Y_i , \hat{Y}_i — estimated value of Y by the empirical curve at point X_i , n — number of samples, X_{\max} — maximum MX_j , X_{\min} — minimum MX_j , E — extent of averaging.

The same step intervals, extents of averaging, and corrective coefficients were used in working out the curves expressing relationships bet-

were the frequency of the species and one of the environmental factors. Thus, the estimated mean value of the frequency of the species (FR_j) at point MX_j was calculated as

$$FR_j = \sum_i Q'_{ij} / \sum_i Q_{ij}, \quad (8)$$

where $\sum_i Q'_{ij}$ = the sum of Q_{ij} in case $Y_i > 0$ within $MX_j \pm E$.

All calculations were programmed in GBASIC and performed on a computer "Apple II".

Results and discussion

The cosmopolitan planktic freshwater species *F. longiseta* is also widely distributed in coastal areas and bays of the Baltic Sea (Remm, 1987). It feeds predominantly on detritus and bacteria (Pourriot, 1977; Hakkari, 1972) and is considered to be an indicator of β - α mesosaprobic and eutrophic conditions in lakes and coastal areas of the Baltic Sea (Berzins, 1949; Gannon, Stemberger, 1978; Melvasalo, Viljamaa, 1975; Mäemets, 1983; Pejler, 1965, 1983; Radwan, 1976; Sládeček, 1983; Кутикова, 1970; Лагановская, 1974; Макрушин, 1974; Мяметс, 1979). A significant positive correlation between the occurrence of *F. longiseta* and the total phosphorus, $KMnO_4$ consumption and lignin concentration was found in Finnish lakes (Hakkari, 1978). On the ground of the data from the Haapsalu Bay the abundance of *F. longiseta* correlated positively with the mean chlorophyll *a* concentration of the growth period and water temperature, a relatively weak negative correlation was found with the depth of the sampling station (Ремм, 1984).

The strongest relationship in the Matsalu Bay was observed between *F. longiseta* log abundance and season (Fig. 2A). Although the raw abundance varied from 0 to 238 000 ind./m³ the relationship is statistically highly significant ($P > 0.999$) (the Table). The relationship curve reveals an evident maximum of the mean abundance in the first half of June. It is possible that the maximum of *F. longiseta* is related to the bloom and subsequent decay of *Cladophora* in the eastern and central parts of the bay during this subseason. Bottom macrophytes develop extensively in the relatively shallow Matsalu Bay later in summer, apparently utilizing a great amount of inflowing biogens, which, together with the sedimenta-

Statistics on the empirical relationships between *F. longiseta* logarithmic abundance and some environmental factors

Environmental factor and its unit	Zero-abundances	<i>n</i>	<i>E</i>	<i>S</i>	<i>F</i>	<i>P</i>	<i>R</i>
Season, day	incl.	187	30	10	21.31	>0.999	0.609
	excl.	80	30	10	2.51	>0.95	0.381
Salinity, ‰	incl.	187	1.25	0.5	8.94	>0.999	0.466
	excl.	80	1.25	0.5	2.71	>0.95	0.414
Log chl <i>a</i> , log µg/l	incl.	140	0.25	0.1	7.50	>0.999	0.460
	excl.	58	0.25	0.1	1.21	<0.70	0.303
Water temperature, °C	incl.	144	3	1	3.11	>0.95	0.337
	excl.	62	3	1	0.89	<0.70	0.262
pH	incl.	135	0.5	0.1	2.72	>0.95	0.284
	excl.	51	0.5	0.1	1.09	<0.70	0.301

(*n* — number of samples, *E* — extent of the averaging, *S* — step interval, *F* — F-ratio, *P* — level of significance, *R* — correlation index)

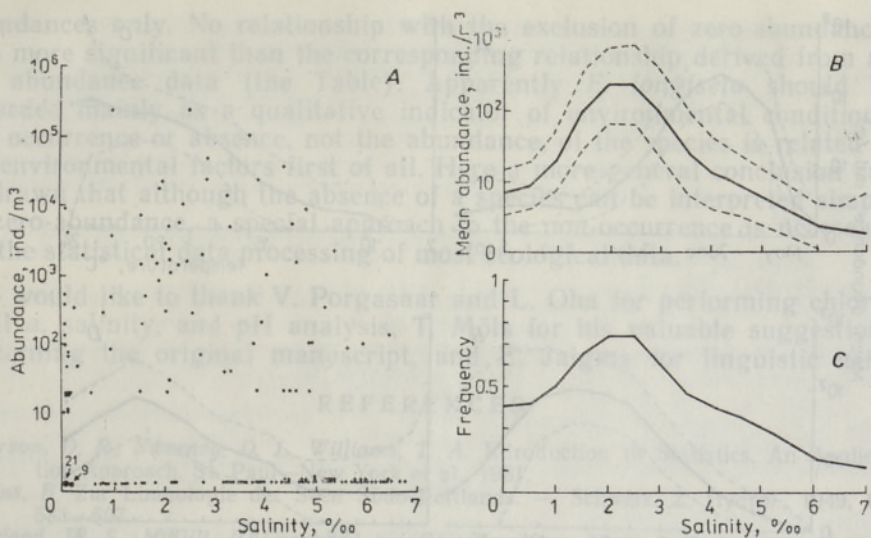


Fig. 1. Relationships between water salinity, *F. longiseta* abundance and frequency (A — scatter diagram with *F. longiseta* abundance data, B — *F. longiseta* mean abundance with confidence limits, C — *F. longiseta* mean frequency of occurrence).

tion of detritus, leads to the weakening of eutrophic characteristics in July and August when other conditions are favourable for the development of *F. longiseta*.

The second strongest relationship was found between *F. longiseta* and water salinity. A scatter diagram of abundance and salinity data is presented to provide a visual evaluation of the modified moving average method (Fig. 1). As a freshwater species *F. longiseta* may be expected to have highest abundance at low salinities but in the Matsalu Bay its optimum salinity is 1.5–3‰ (Fig. 1). Evidently the inflowing water, rich in humic substances, is not suitable for this species. We have found only single specimens from the reedbed channel of the Kasari River, the main fresh-water inflow into the bay. Literature data on the salinity tolerance of *F. longiseta* are very scarce. K. M. Levander (1915) estimated maximum salinity for *F. longiseta* as 4.43‰. We have found single specimens at up to 6.5‰ in the Matsalu Bay.

Since *F. longiseta* is referred to as an indicator of eutrophy, the relationship with the essential eutrophy parameter chlorophyll *a* is of special interest. The relationship curve points to the maximum mean abundance of *F. longiseta* at 4–10 µg/l of the chlorophyll *a* concentration (Fig. 2B). However, the steep decline of the mean abundance curve at chlorophyll *a* concentrations above 10 µg/l is not sufficiently confirmed, as indicated by the wide confidence limits. There were only 9 samples with chlorophyll *a* concentration above 10 µg/l, while 4 of these were collected in May when the phytoplankton biomass is generally higher. In addition, the abundance of *F. longiseta* varied especially in samples with chlorophyll *a* concentration above 10 µg/l. On the other hand, the decreasing tendency of abundance is also evident at higher pH values (pH > 8.7) (Fig. 2D). This phenomenon is in discordance with V. Sládeček's (1983) classification where *F. longiseta* is included into the group of alkaline species. It is known that high pH values refer to the high primary production and, hence, indicate eutrophy. Thus, our data refer to *F. longiseta* as an indicator of mainly mesotrophic water; however, this question needs further study.

The relationship between *F. longiseta* abundance and water tempera-

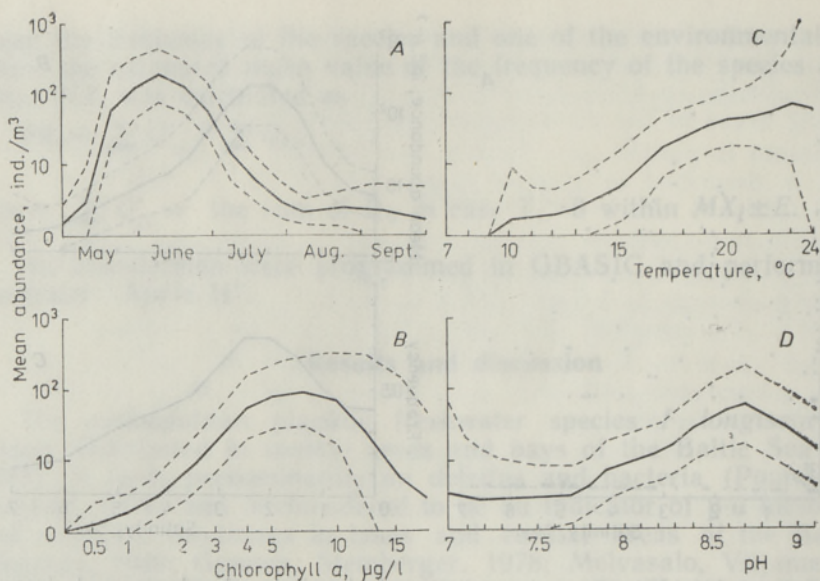


Fig. 2. Relationships between *F. longiseta* mean abundance and some environmental factors (A — season, B — chlorophyll *a* concentration, C — water temperature, D — water pH). Dotted lines indicate the confidence limits of the mean abundance.

ture gives evidence of the preference of warmer water by *F. longiseta*. The species has never been found in the Matsalu Bay at water temperature below 12°C according to our data, and the mean abundance increases gradually as the temperature rises (Fig. 2C).

As can be expected, no relationship was found between the *F. longiseta* abundance and water depth at the sampling station.

It can be seen that the frequency curves are very similar to the mean abundance curves (Fig. 3). To elucidate the role of zero-abundances the mean abundance curves were calculated with the inclusion of above-zero

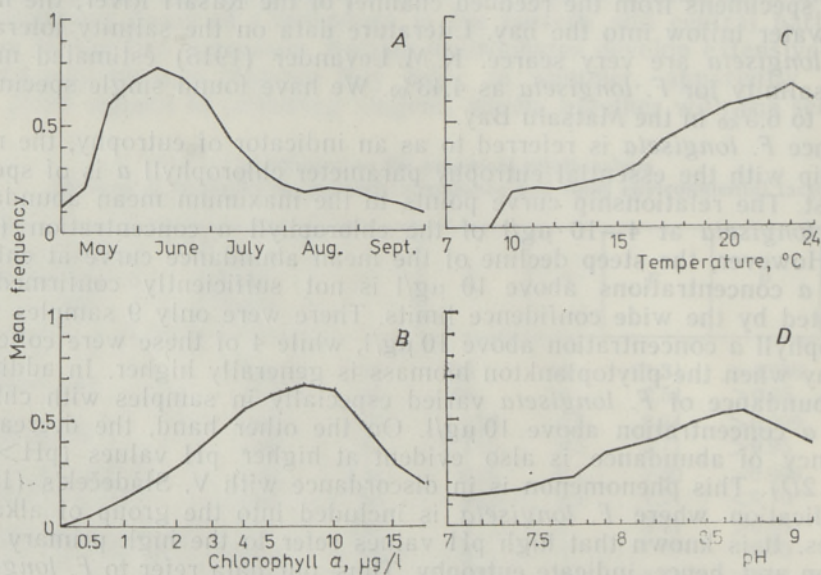


Fig. 3. Relationships between *F. longiseta* mean frequency and some environmental factors (A — season, B — chlorophyll *a* concentration, C — water temperature, D — water pH).

abundances only. No relationship with the exclusion of zero-abundances was more significant than the corresponding relationship derived from all the abundance data (the Table). Apparently *F. longiseta* should be regarded mainly as a qualitative indicator of environmental conditions. The occurrence or absence, not the abundance, of the species is related to the environmental factors first of all. Here a more general conclusion can be drawn that although the absence of a species can be interpreted simply as zero-abundance, a special approach to the non-occurrence is necessary in the statistical data processing of most ecological data.

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Academy of Sciences of the Estonian SSR,
Institute of Zoology and Botany

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Kalle REMM

STATISTILINE MEETOD ÕKOLOOGILISTE SEOSTE HINDAMISEKS FILINIA LONGISETA (EHR.) (ROTATORIA) NÄITEL

Töös on esitatud meetodika kahe muutuja (näiteks liigi arvukuse ja mingi keskkonnateguri (gradiendi) vahelise seose leidmiseks, kusjuures seose tüüp ja kuju ei ole ette antud. Esitatud meetodika põhineb klassikalisel aegridade silumise meetodil libiseva keskmise abil. Meetodit on täiendatud paranduskoeffitsiendiga ja rakendatud ka teistele keskkonnateguritele peale aastaaja. Kõnealuse meetodika järgi on Matsalu lahest kogutud andmete põhjal selgitatud kerilooma *Filinia longiseta* (Ehr.) arvukuse ja esinemissageduse sõltuvus mõnedest keskkonnateguritest. Statistiliselt usaldatavad seosed õnnestus leida *F. longiseta* logaritmitud arvukuse ja järgmiste keskkonnategurite vahel: aasta-aeg, soolsus, vee klorofüllil *a* sisaldus, vee temperatuur, vee pH. Seos puudus *F. longiseta* arvukuse ja proovivõtukohta sügavuse vahel. Seosed liigi logaritmitud arvukuse ja kõigi analüüsitud keskkonnategurite vahel olid tunduvalt nõrgemad, kui arvesse võeti vaid need proovid, kus liik esines. Seega võib *F. longiseta*'t pidada eelkõige keskkonnatingimuste kvalitatiiivseks indikaatoriks. Keskkonnateguritest sõltub põhiliselt liigi esinemine või puudumine, mitte selle arvukus.

Kalle REMM

СТАТИСТИЧЕСКИЙ МЕТОД ДЛЯ АНАЛИЗА ЭКОЛОГИЧЕСКИХ СВЯЗЕЙ, ИЗЛОЖЕННЫЙ НА ПРИМЕРЕ ДАННЫХ ЧИСЛЕННОСТИ FILINIA LONGISETA (EHR.) (ROTATORIA)

Изложена методика для анализа зависимостей между двумя переменными. При этом форма зависимости предварительно не установлена. Используется метод скользящей средней, применяемый в основном для выравнивания временных рядов, который усовершенствован коэффициентом поправки (Q_{ij}). Коэффициент поправки дифференцирует относительный вклад конкретных значений функциональной переменной (Y_i) в скользящей средней в соответствии с расстоянием ($MX_j - X_i$) от середины (MX_j) зоны усреднения ($MX_j \pm E$) по формуле $Q_{ij} = 1 - (MX_j - X_i)^2 / E^2$. Статистически достоверные зависимости найдены между средней численностью *F. longiseta* (трансформированной по формуле $N_i = \log_{10}(n_i + 1)$) и следующими факторами среды: временем года, соленостью, содержанием хлорофилла *a*, температурой воды и pH. Зависимости от глубины станции не было обнаружено. Зависимости со всеми факторами окружающей среды оказались более слабыми, если в расчетах использовали только те пробы, где рассмотренный вид встречался. Итак, можно сделать вывод, что *F. longiseta* является в основном качественным, а не количественным индикатором условий среды.