

ESTIMATION OF TAYLOR'S POWER LAW PARAMETERS *a* AND *b* FOR TIDAL MARSH MACROBENTHIC SPECIES

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ABSTRACT. In the Cananea region of southeastern Brazil, *Spartina alterniflora* marshes colonize tidal flats fringing mangrove woodlands and displaying a zonation typical of monocultures. The pattern observed can be explained by the combined effects of organism resistance to emersion and physical dependence on the plants as habitat. In this context, it is interesting to quantify the aggregation index for the dominant species associated with the salt marsh. A tool which enables us to do it is Taylor's power law, which combines the mean and the variance distributions of species in a known area. From August 1988 to January 1989, ten random samples were taken monthly from the lower and upper marshes using a 20 cm diameter corer (0.03 m²) at a depth of 10 cm. The five most representative species of the system were selected for further analysis, and for each of these, Taylor's power law parameters were calculated. Epifaunal species present aggregation indexes approaching randomness. The aggregation indexes for the infaunal species were observed to have consistently high values even in clearly different conditions of population density and availability of organic matter. The smaller number of infauna forms in the lower marsh as compared to the upper marsh does not point to a competitive disadvantage since there is no alteration in *b* values. For the infauna species only, the value of *a* shows a sharp decrease from the lower to the upper marsh.

Keywords: Salt marsh macrobenthic fauna, spatial distribution, Taylor's power law.

Cálculo de los parámetros *a* y *b* de la Ley de Poder de Taylor para especies macrobentónicas de marisma

RESUMEN. En la región de Cananea al SE de Brasil, el pasto *Spartina alterniflora* coloniza los bajos de marea de las marismas que rodean los manglares, mostrando una zonación típica de monocultivos. El patrón observado se puede explicar por el efecto combinado de la resistencia de los organismos a la exposición al aire y a la dependencia física de las plantas como hábitat. En este contexto, es interesante cuantificar el índice de agregación para las especies dominantes asociadas a la marisma. Una herramienta que nos permite hacerlo es la Ley de Poder de Taylor, la cual combina las distribuciones promedio y de la varianza de las especies en un área conocida. De agosto de 1988 a enero de 1989, diez muestras mensuales fueron tomadas aleatoriamente de la marisma superior e inferior mediante un nucleador de 20 cm de diámetro (0.03 m²) a una profundidad de 10 cm. Las cinco especies más representativas del sistema fueron elegidas para un análisis posterior y se calcularon los parámetros de la Ley de Poder de Taylor a cada una de ellas. Las especies de epifauna presentaron un índice de agregación cercano a la aleatoriedad. Los índices de agregación de las especies de la endofauna mostraron consistentemente altos valores, incluso en diferentes condiciones de densidad de población y de disponibilidad de materia orgánica. El reducido número de formas de endofauna en la marisma inferior, comparada con la superior, no apunta a una desventaja competitiva, ya que no hay alteraciones en los valores de *b*. Solo para las especies de endofauna, el valor de *a* mostró un agudo decremento desde la marisma inferior hacia la superior.

Palabras clave: Marisma, macrofauna bentónica, distribución espacial, Ley de Poder de Taylor.

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INTRODUCTION

In southeastern Brazil, *Spartina alterniflora* Loisel, 1807 marshes colonize tidal flats fringing mangrove woodlands and display a

zonation typical of monocultures, with different growth forms and shoot densities characterizing the lower and upper marshes, each presenting different community organizations as to mean densities and faunal dominance. This

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herbaceous plant community has different structure above and below the mean high water (MHW). Below MHW the assembly is dominated by epifaunal species such as *Sphaeromopsis mourei* Loyola & Silva, 1960, *Parhyale hawaiiensis* Dana, 1853 and *Littorina angulifera* Lamarck, 1822, while above MHW it is dominated by the infauna species *Isolda pulchella* Fritz Muller, 1858 and *Nereis oligohalina* Fritz Muller, 1858. The pattern observed can be explained by the combined effects of organism resistance to exposure and physical dependence on the plant as substratum (Flynn *et al.*, 1998). The epifaunal crustaceans are associated with the *S. alterniflora* blades and are dominant in the lower marshes because of the adequate period of immersion. Infauna organisms were dominant in the upper marshes because they can better resist the prolonged exposure to air and benefit from the high plant biomass there (Flynn *et al.*, 1996; Flynn *et al.*, 1998).

Taylor's Power Law (TPL) is a well documented relation between the average and the variance of ecological populations. Its use has been amply discussed and it provides useful information regarding the dispersal patterns of organisms (Gaston *et al.*, 2006). Taylor (1961) first used the formula derived from the negative binomial distribution to measure the level of aggregation. In this equation, m and S^2 represent the first and the second moments respectively, which are statistical terms denoting the mean and the variance of the binomial negative probability function (Ascombe, 1949). Taylor expected k to be a characteristic of each species but found that k is not always independent of the mean.

Taylor originally suggested that a and b were fixed for each species. Examining sets of samples of various species, Taylor found that the mean was related to the variance according to the power law $S^2 = a m^b$ suggesting that both, a and b are population characteristics. With log-transformed data, the power law in this case is represented by a straight line of slope b and y-intercept a . The maximum value of the log of the variance is obtained when b equals 2, $\log S^2_{\max} = \log a + 2 \log m$. Biologically we can interpret S^2_{\max} as the maximum variance expected for a given number of population sets of a chosen two dimensional area ($b = 2$) sampled at a specific location. However, it was found that for different methods of sampling a changes while b remains constant for a

given species (Taylor, 1970). The slope b is considered an aggregation index. The slope equals unity for a random distribution; it is lower than unity in the case of a regular distribution and greater than unity in the case of an aggregated distribution. In a study of aphid distributions with fixed sample methodology (Taylor, 1977; Taylor *et al.*, 1979), a was affected by the host plant distribution, leading to the conclusion that a can be used as an environmental stress index. In spite of the evidence, the behavior of a and b are not completely understood. A full explanation and review of TPL with detailed derivations can be found in Tokeshi (1995) and Eisler *et al.* (2008).

Our objective was to obtain TPL's parameters (a and b) for five macrofaunal species from empirical data collected in a tidal flat colonized by *Spartina alterniflora* at Cananeia lagoon estuarine system (Flynn *et al.*, 1998), and estimating their values for the lower and upper marshes.

MATERIAL AND METHODS

Cananeia lagoon estuarine system is located in the State of São Paulo, southeastern Brazil. A complete description and characterization of the system is given in Schaeffer-Novelli *et al.* (1990). Pure stands of *Spartina alterniflora* form the bulk of the vegetation. Samples were taken randomly from the lower and upper marshes at Ponta do Arrozal, which contains the largest marsh in the region, covering an area of 25 km². Faunal samples were taken monthly from August 1988 to January 1989 consisting of 10 randomly chosen replicates taken with a 20 cm diameter corer (0.03 m²) at a depth of 10 cm. Standing dead and live shoots of *S. alterniflora* were clipped at ground level and visually searched for epifaunal organisms. Samples were sieved through 1.0 and 0.5 mm meshes. The organisms were then fixed in 10% formalin and preserved in 70% ethanol. All specimens were identified at the lowest possible taxonomic level and counted under a dissecting microscope.

Five of the total 60 species were used, the epifaunal crustaceans *Sphaeromopsis mourei* and *Parhyale hawaiiensis*, dominant in the lower marsh, *Nereis oligohalina* and *Isolda pulchella*, dominant in the upper marsh, and *Littorina angulifera* common in both. A total of 14,803 specimens were obtained for these 5 species (*S. mourei*, lower marsh = 1,417; *P. hawaiiensis*, lower marsh = 965, upper marsh

= 202; *I. pulchella*, lower marsh = 334, upper marsh = 5,950; *N. oligohalina*, lower marsh = 584, upper marsh = 3,650; *L. angulifera*, lower marsh = 441, upper marsh = 1,260). A two-way analysis of variance with replication was used in order to test for differences in abundance in each of the top five species by site and month. The power of the test was estimated to be around 0.78 based on the method described by Zar (1999) (Flynn *et al.*, 1998). To estimate the parameters *a* and *b* of TPL a logarithmic transformation of the data was performed for each species set. The coefficient of determination (Pearson *r*-squared, R^2) was used as an indicator of quality of the linear regression. The angular coefficient (*b*) and the y-intercept ($\log a$) of each species was tested with the 2-tailed Student's *t*-test ($\alpha = 0.05$) with *n*-2 degrees of freedom.

RESULTS

The Taylor's constants calculated for each macrofaunal species were the slope *b* (aggregation index) and the y-intercept *a* (environmental stress index) (Table 1). For the infaunal species *I. pulchella* and *N. oligohalina* the aggregation index values were around 2. For epifaunal species and for *S. mourei*, present only at the lower marsh, the aggregation index was lower than 2.

The environmental stress indexes for the infaunal species were significantly different for the two sites. For *I. pulchella* the *a* value in the lower marsh was higher than in upper marsh. The same behavior was observed in *N. oligohalina*. Thus, for infaunal species, there is a clear decrease in *a* with increasing distance to water. Epifaunal species did not show the same trend. *L. angulifera* in the lower marsh show a higher value than in the upper marsh. *P. hawaiiensis* showed similar values between sites and *S. mourei* presented an environmental stress index value relatively high.

The log transformed TPL for the macrofaunal species of the lower and upper marshes is presented in Figure 1. The linear slope represents the aggregation index, and the y-intercept value the environmental stress index.

The infaunal species *I. pulchella* and *N. oligohalina* presented higher and more stable mean density values at the upper marsh throughout the sampling period, while epifaunal species *P. hawaiiensis* and *L. angulifera* presented clear variations in mean densities,

Table 1. Taylor's parameters resulting in the linear equation $\log S^2 = b \log m + \log a$ for the five macrofaunal species, with the determination coefficient (R^2) and confidence interval (CI).

| | Lower Marsh | | |
|-----------------------|---------------|---------------|-------|
| | <i>a</i> ± CI | <i>b</i> ± CI | R^2 |
| <i>I. pulchella</i> | 2,388 ± 0,186 | 2,139 ± 0,355 | 0.899 |
| <i>N. oligohalina</i> | 1,770 ± 0,440 | 2,094 ± 0,566 | 0.843 |
| <i>L. angulifera</i> | 1,982 ± 0,047 | 1,719 ± 0,068 | 0.968 |
| <i>P. hawaiiensis</i> | 4,207 ± 0,037 | 1,583 ± 0,029 | 0.983 |
| <i>S. mourei</i> | 3,606 ± 0,128 | 1,134 ± 0,084 | 0.937 |
| | Upper Marsh | | |
| | <i>a</i> ± CI | <i>b</i> ± CI | R^2 |
| <i>I. pulchella</i> | 0.942 ± 2,470 | 2,010 ± 0,658 | 0.810 |
| <i>N. oligohalina</i> | 0.456 ± 1,586 | 2,123 ± 0,514 | 0.859 |
| <i>L. angulifera</i> | 1,122 ± 0,109 | 1,780 ± 0,075 | 0.967 |
| <i>P. hawaiiensis</i> | 4,305 ± 0,189 | 1,214 ± 0,425 | 0.585 |

both between sites and throughout the period. Epifaunal species are dominant in the lower marsh, mainly because of the smaller infaunal abundance. *S. mourei* occurs exclusively in the lower marsh (Table 2).

DISCUSSION

The positive correlation of the mean densities of *N. oligohalina* and *I. pulchella* with the plant biomass (Lana & Guiss, 1992) and their preference for habitats with high plant biomass in areas where tide levels allows a denser colonization by *S. alterniflora* (Flynn *et al.*, 1996) does not translate into different values of species aggregation index. *I. pulchella* and *N. oligohalina* present high values of the aggregation index *b*, both for high population densities in the upper marsh and for low population densities in the lower marsh. The aggregation indexes for the infaunal species show consistently high values even in clearly different conditions of population density and availability of organic matter. The aggregation of these infaunal species to single stems or groups of stems of salt marsh vegetation seems to protect them against predatory action. Their sedentary habit as detritus feeders with low selectivity, which does not call for great displacements, promotes their continuous permanence in the habitat and, consequently, their aggregated pattern (Rader, 1984). *L. angulifera*, *P. hawaiiensis* and *S. mourei* present aggregation indexes below 2. The first two species show a more highly aggregated distribution than the third, which is almost random. In natu-

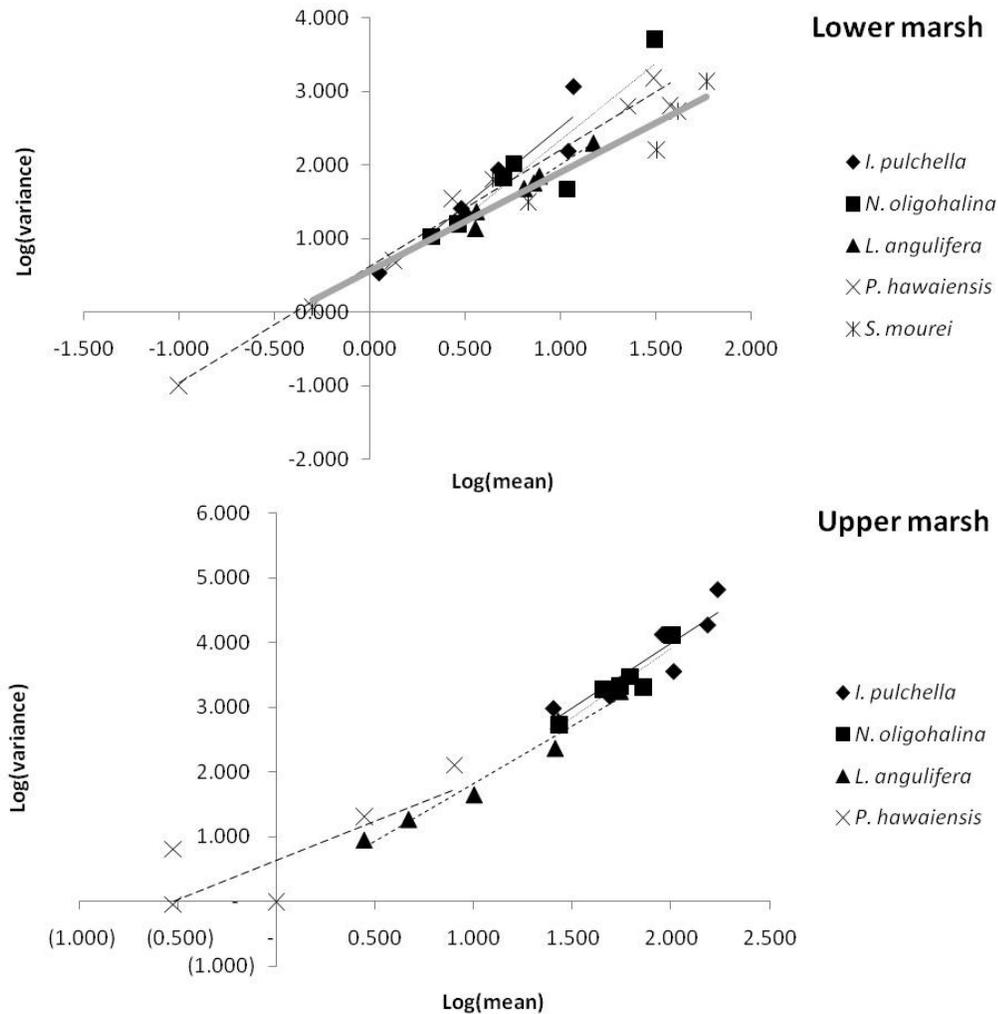


Figure 1. Relationship between the log transformed variance and log transformed mean abundance of the macrofaunal species, with the adjusted linear equation for lower and upper marshes.

re, the aggregation index b for true randomness ($b = 1$) is one possible value within a continuous range from $b = 0$ (for regular distribution) to $b = 2$ (highly aggregated distribution). TPL method was applied to more than 400 sets of species data with b varying from 0.9 to 2.6, with a higher concentration of values between 1.0 and 1.8 (Taylor & Woiwod, 1982). Values of b higher than 2 are due to errors caused by the great number of zeros in the ecological data (Tokeshi, 1995). The values we obtained varied from 1.134 to 2.139. With the exception of *S. mourei*, exclusively of the lower marsh, the aggregation indexes for the species considered were very similar in the upper and lower marshes. Therefore, b seems to describe an intrinsic biological property of the macrofaunal species considered here, consis-

tent with the concept of He and Gaston (2003) of a model considering the abundance-variance occupancy as an explanation for the occurrence of diverse species assemblages at different scales. There is obvious variation about the interspecific abundance–variance relationship (Gaston *et al.*, 2006).

The initial impression of homogeneity created by a monospecific bed of *S. alterniflora* masks the reality of a truly patchy ecosystem. The infaunal species are clearly the numerical dominant forms in the upper marsh, while in the lower marsh the epifaunal forms are dominant (Flynn *et al.*, 1998). *N. oligohalina* and *I. puchella* are in numerical disadvantage in the lower marsh. However, this is not reflected in the aggregation index values. As pointed out by Taylor (1961) in his support of

Table 2. Variation range and results of 2-way ANOVA evaluating effect of site and time on each of the five macrofaunal species considered (lower marsh vs. upper marsh). NS: non significant difference, $p>0.05$; $0.05>p>0.01$; $**p<0.01$; $***p<0.001$.

| Species | Variation range (0.03m ²) | | Total average | | Between Site | F-value Time | Interaction |
|-----------------------------|------------------------------------------|----------------|----------------|----------------|-----------------|--------------------|--------------------|
| | Lower marsh | Upper marsh | Lower marsh | Upper marsh | (df = 1) | (df = 5) | |
| <i>Sphaeromopsis mourei</i> | 0-376 | 0 | 148.2 | 0 | 41.07*** | 8.99*** | 8.99*** |
| <i>Parahyale hawaensis</i> | 0-184 | 0-38 | 73.6 | 10.8 | 20.48*** | 10.11*** | 5.67*** |
| <i>Littorina angulifera</i> | 11-92 | 14-174 | 47.6 | 104.6 | 6.49** | 4.16*** | 1.82 ^{NS} |
| <i>Isolda pulchella</i> | 4-51 102-445 | | 23.2 | 352.6 | 35.66*** | 1.85 ^{NS} | 1.73 ^{NS} |
| <i>Nereis oligohalina</i> | 7-60 141-348 | | 37.2 | 305.0 | 39.24*** | 1.18 ^{NS} | 0.70 ^{NS} |

the TPL parameter b as an aggregation index, it is plainly desirable that an index of population structure should be the same for different population densities, unless some actual change in behavior is involved. When we compare infaunal polichaets densities for the lower and the upper marshes, we find that the latter is 11.8 times higher (Flynn, 1998). We saw no significant difference in b values.

Would the numerical decrease of infaunal forms point to a competitive disadvantage in the lower marsh as compared to the upper marsh? It seems that the answer to this question is no, since there is no significant variation in b values. Based on results obtained from computer simulations Kilpatrick and Ives (2003) associated a strong competition force or a smaller carrying capacity K to a TPL slope decrease. In their simulation, as the average slope decreases from 2 to 1, the competition coefficient increases from 0 to 0.16, so that competitive interactions are also sensitive to population fluctuations and TPL parameters. Nevertheless, the infaunal decline in abundance in the lower marsh could be caused by a decrease in carrying capacity K , since, the more common species are supposedly associated with higher carrying capacities. The lower *S. alterniflora* densities and the consequently lower availability of organic matter in the lower marsh, coupled with the presence of a higher number of species, seem to interfere with the infaunal species abundance, so that the lower spatial occupation can be related to a greater environmental stress. Supporting this view is

the value of a for infaunal species which is clearly smaller in the upper marsh than in the lower marsh.

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