

THE TIDEPOOL ALGA *CYSTOSEIRA HUMILIS* ON AN OCEANIC ISLAND EXHIBITS PARTIAL ADHERENCE TO TAYLOR'S LAW

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Gómez-Alcañiz, A. & R. Riera (2025). El alga de charcos *Cystoseira humilis* en una isla oceánica exhibe una adherencia parcial a la Ley de Taylor. *Vieraea* 48: <https://doi.org/10.31939/vieraea.2025.48.15>

ABSTRACT: Taylor's Law is an empirical relationship between the variance (s^2) and the mean (m) of abundance estimates described by the equation $s^2 = am^b$, where b is the aggregation index. From this relationship it is possible to quantify the degree of aggregation. The present study checks the validity of Taylor's Law using a benthic species, *Cystoseira humilis* in the intertidal pools of the island of Gran Canaria (NE Atlantic Ocean). Eight

intertidal pools were sampled in three locations with a 25 x 25 cm grid. Thallus abundance and small, medium and large scale spatial variation were determined. The total number of thalli samples was 24,329 among the eight studied tide pools. The shallower the tide pool, the fewer thalli per stipe were found. *Cystoseira humilis* showed a regular distribution, and was not fully adapted to Taylor's Law.

KEYWORDS: Intertidal pools / macroalgae / *Cystoseira* / Theory / Taylor's law.

RESUMEN: La Ley de Taylor es una relación empírica entre la varianza (s^2) y la media (m) de las estimaciones de abundancia, descrita por la ecuación $s^2 = amb$, donde b es el índice de agregación. A partir de esta relación, es posible cuantificar el grado de agregación. El presente estudio verifica la validez de la Ley de Taylor utilizando una especie bentónica, *Cystoseira humilis*, en charcos intermareales de la isla de Gran Canaria (NE del Océano Atlántico). Se muestrearon

ocho charcos intermareales en tres localidades, utilizando una cuadrícula de 25 x 25 cm. Se determinaron la abundancia de talos y la variación espacial a pequeña, mediana y gran escala. El número total de talos muestreados fue de 24.329 entre los ocho charcos estudiados. El número de talos por estipe fue inferior en los charcos más someros. *Cystoseira humilis* mostró una distribución regular y no estuvo completamente adaptada a la Ley de Taylor.

PALABRAS CLAVE: Pozas intermareales / macroalgas / *Cystoseira* / Teoría / Ley de Taylor.

INTRODUCTION

Ecology studies the relationship between living beings and the environment, in which models, equations and laws are used. The first and second laws of thermodynamics, the law or rule of stoichiometry, Darwin's Law of natural selection (Lawton 1999), and Taylor's Law (Southwood and Southwood 1966) are examples of laws. Taylor's law was popularized by Lionel Roy Taylor in 1961. The name "Taylor's Law" was imposed by Southwood and Southwood in 1966. This law is based on the empirical relationship between the sample, spatial or temporal variance (s^2) and the sample mean (m) of estimates of abundance of populations of individuals (Taylor 1961; Teixeira-Roth and Sánchez-Infantas 2006). If individuals are independently distributed, then the Poisson distribution applies and the sample mean is approximately equal to the same variance. However, individuals in natural populations are not independent of each other; mutual attraction or variation in habitat suitability to aggregation makes the variance greater than the mean ($s^2 > m$) (Taylor 1961). Taylor (1961) relates the variance and the mean through a power law:

$$s^2 = a^1 m^{b^1} \quad (1)$$

where a and b are characteristics of the studied population, in addition to being parameters to be statistically estimated (Teixeira-Roth and Sánchez-Infantas 2006). Specifically, b is the aggregation index, which is specific for each species (Redfearn and Pimm 1988). These authors proposed replacing the variance with the coefficient of variation (CV) as a measure of population variability, since it admits the comparison between different species and, moreover, it is not affected by the zeros because it does not require that the data be transformed (McArdle et al. 1990; Giraldo et al. 2002; Teixeira-Roth and Sánchez-Infantas 2006).

$$CV = a_2 m^{b_2} \quad (2)$$

The following regression is derived from this equation:

$$CV = a + b \cdot m \quad (3)$$

From Taylor's Law it is possible to quantify the degree of aggregation and understand the spatio-temporal distribution patterns of the populations (Teixeira-Roth and Sánchez-Infantas 2006). Aggregation depends on the ecology of the species, but also on the distribution of resources in the environment and on

the management of populations (Laguna-Fernández 2015). Variation related to mean power laws has also been demonstrated in several non-ecological systems, such as in medicine, in cancer metastasis studies (Kendall and Jorgensen 2011). Taylor's Law has been widely applied in the field of ecology (Taylor, 2019). It has been studied in insects (Nestel et al. 1995), bacteria (Ramsayer et al. 2012), macroinvertebrates of rivers (Monaghan 2015), and aquatic parasites (Cohen et al. 2017) of the terrestrial environment. Also, in oak communities (*Quercus* spp.) (Cohen et al., 2012), in tropical forests (Xu et al., 2021) and to understand the spatio-temporal variability of the plant community, as well as its response to environmental conditions (Teixeira-Roth and Sánchez-Infantas 2006). In the marine environment, articles on this law include studies on benthic invertebrates (Kristensen et al. 2013), on the ringed seal (*Phoca hispida*) (Kingsley 1989), on fish associated with *Posidonia oceanica* meadows of the Mediterranean Sea (Mouillot et al. 1999), and commercial fish such as tiger fish (*Hydrocynus vittatus*), *Serranochromis codringtonii*, *Synodontis zambezensis* and tilapia (*Oreochromis mortimeri*) (Fujiwara and Cohen 2014; Xu 2016). In addition, Taylor's Law has been tested on metazoans of heterogeneous lifestyles (free-living and parasitic) in the same habitat (Lagrue et al., 2015). Additionally, Taylor's law can be used to find out if initial densities in an irregular environment affect the occurrence of abrupt transitions, in a Taylor's law birth and death model (Jiang et al., 2014).

Here we study Taylor's Law in coastal communities, using the alga *Cystoseira humilis* (Schousboe ex Kützing, 1860) from the intertidal pools of the Northwest, North and East of the island of Gran Canaria. Tide pools are affected by various environmental factors, such as tides, swell and wave height and wind speed and direction (Ramírez et al. 2008). The present study focuses on the furoid *Cystoseira humilis* because it is abundant in intertidal pools, although the distribution of the genus *Cystoseira* is being increasingly affected by global warming (Buonomo et al. 2018). Specifically, the distribution of *C. humilis*, decreased compared to the 90s, extends to all the islands belonging to Macaronesia, being abundant in the Canaries (**Fig. 1**). The study of spatial distribution of macroalgae are pivotal to unveil the community assembly of associated species such as epifauna and epiflora, as well as, the patterns of distribution, abundance and diversity of species of these associated communities (Benedetti-Cecchi and Cinelli, 1997).

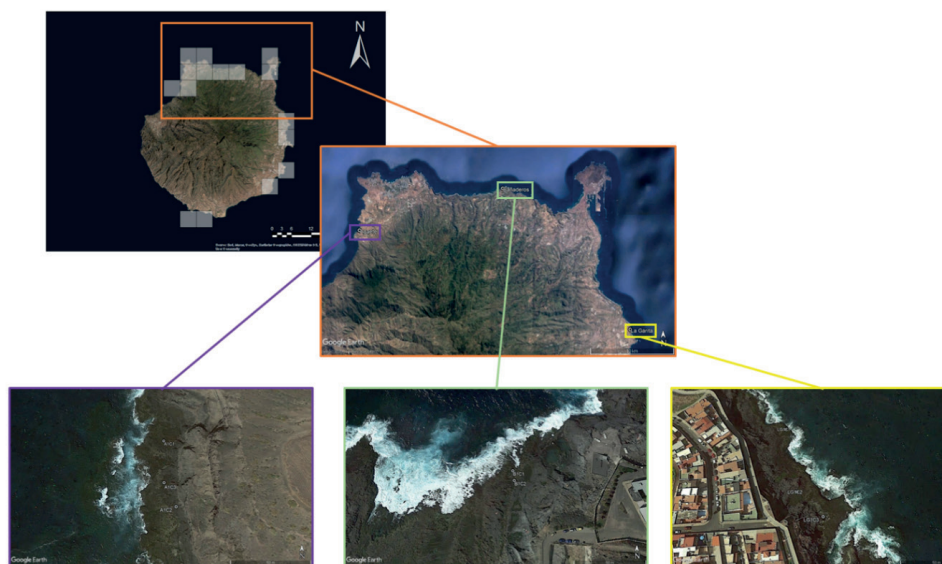


Figure 1: Map of the island of Gran Canaria with the sampling locations. Source: Google Earth, 2021.

MATERIAL AND METHODS

• Study area and sampling procedures

Three suitable locations were selected, one in the Northwest (Agaete), in the North (Bañaderos) and in the East (La Garita) (**Fig. 1**). In each location, three tide pools were chosen, except in Bañaderos, where only two were sampled. All studied tide pools were dominated by the furoid algae *Cystoseira humilis*. In each sampled pool, three areas were selected, and at each area, five 25*25 cm quadrats (subdivided by 5*5 cm subgrids) were sampled; thus, a total of 15 quadrats (375 subgrids) were sampled at each pool. Each quadrat was randomly placed, and the stypes - a stemlike structure in algae- and thalli -plant body of algae- were counted by hand. All selected pools were shallow (< 1m depth) to facilitate sampling.

• Taylor's law

Through a linear regression, using Equation 2, the value of a and b is obtained. Depending on the value of b , the sample will show a type of distribution. A slope greater than two ($b > 2$) corresponds to an aggregated population, a slope less than two ($b < 2$) corresponds to a population that is regularly distributed, and a slope equal to two ($b = 2$) means that they can be distributed randomly (Soberón

and Loevinsohn, 1987). In the case that b is different from 2, the variability of the population (as measured by the CV) will depend on the mean abundance, and when b is equal to 2, the variability of the population does not depend on the mean abundance (Soberón and Loevinsohn 1987; McArdle et al. 1990; Teixeira-Roth and Sánchez-Infantas 2006).

- **Statistical analysis**

The mean, standard deviation, variance, and coefficient of variation of each area and each tide pool were calculated. A linear regression was performed to calculate the variables a and b of Taylor's Law, by means of the IBM SPSS Statistics v26.

RESULTS

Cystoseira humilis thalli showed regular, random or aggregated distributions depending on the pool (**Fig. 2**). In Agaete, thalli showed a regular distribution in all sampled pools, but with contrasting results when consider the coefficient determination since b values showed a high variability, i.e. $b=0.92$ (pool 1; $b = 0.28$ (pool 2) and $b = 0.66$ (pool 3) (A1C1) a low degree of aggregation was observed in thalli, consistent with the slope ($b = 0.92$). Thus, thalli showed a regular distribution. In the second pool of Agaete (A1C2) a low degree of aggregation was observed in thalli, which was consistent with the slope ($b = 0.28$). The average coefficient of determination showed a low value ($R^2 = 0.344$, $p = 0.221$). The coefficient of determination widely ranged between these pools, namely $R^2 = 0.6612$ in pool 1; $R^2 = 0.1521$ in pool 2; $R^2 = 0.344$ in pool 3. However, none of them showed significant values, i.e. $p = 0.101$; $p = 0.456$; $p = 0.221$, respectively. In Bañaderos, thalli showed a regular ($b = 1.24$; pool 1) and an aggregated ($b = 3.05$; pool 2) distribution. The coefficient of determination also greatly varied between ($R^2 = 0.387$, $p = 0.278$ in pool 1 and $R^2 = 0.8187$, $p = 0.048$ in pool 2), with a high dispersion of data around the regression line (Fig. 2). In La Garita, thalli showed a regular distribution in all sampled pools. The b values showed slightly varied among pools, i.e. $b = 1.35$ (pool 1); $b = 1.21$ (pool 2); $b = 1.73$ (pool 3). Hence, the same pattern was observed comparing the coefficient of determination, with values ranging between 0.5 and 0.6, i.e. $R^2 = 0.60$ (pool 1); $R^2 = 0.56$ (pool 2); $R^2 = 0.52$ (pool 3) (Fig. 2). The significance test did not show significant values, i.e. $p = 0.101$, $p = 0.132$, $p = 0.144$, respectively). When comparing the slopes among the three localities no significant differences were found ($R^2 = 0.445$, $p = 0.089$).

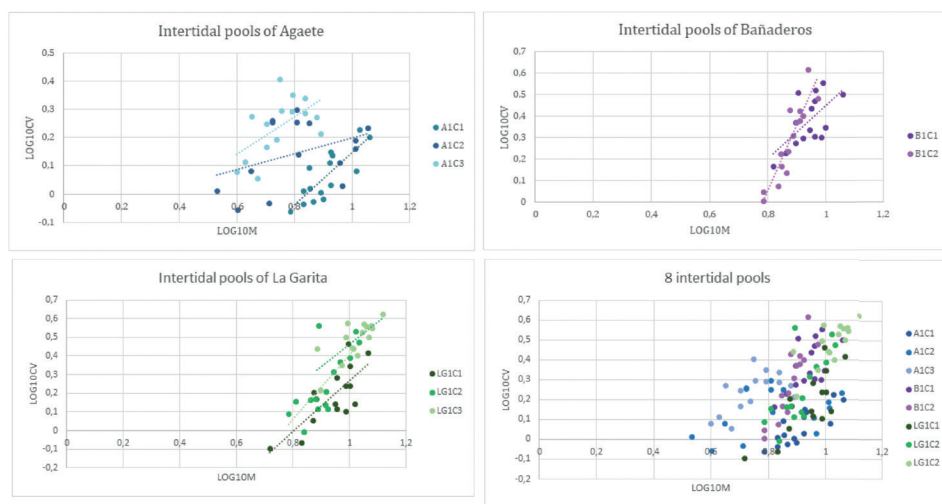


Figure 2: Linear regression A) of the three tide pools belonging to Agaete. B) of the two tide pools located in Bañaderos. C) of the three tide pools belonging to La Garita. D) of the eight tide pools.

DISCUSSION

The distribution pattern shown in all pools was regular, i.e. the individuals are evenly spaced within an area (Begon & Townsend, 2021), with the exception of the second pool of Bañaderos (B1C2) that showed an aggregate distribution, where individuals were found grouped in sectors, and the presence of an individual increases the probability of finding another (Begon & Townsend, 2021).

The aggregate distribution is common in nature, and occurs when a high value of individuals is found in a sector or different sectors. Two clear examples of species that show an aggregated distribution are plankton and small pelagics such as sardine (*Sardina pilchardus*) that forms schools of many individuals. The regular distribution occurs when individuals are evenly spaced within a sector, with small variation in the number of individuals per area. The distribution of random organisms is not homogeneous, since some areas have a higher density, while other areas are more depopulated (Rodríguez-Rey et al. 2013; Begon & Townsend, 2021).

In the Canary archipelago a decline in abundance is being recorded in *Cystoseira* species (Geppi & Riera, 2022). Ocean warming is one of the main drivers of the decrease of fucoids in subtropical regions (Pardi et al. 2000; Riera et al. 2015, Buonomo et al. 2018). To a lesser extent, pollution can cause their displacement and even their local extinction of macroalgae (Devescovi 2015). In addition, several other factors that affect the distribution of *Cystoseira humilis*, include ultraviolet

light (Bentacor et al. 2015), lead and cadmium concentrations (Lozano 2003), interactions with epiphytes, which are favoured by contamination and eutrophication (Otero-Schmitt and Pérez-Cirera 1996; Beleggratis et al. 1999), and invasive species that occupy the same ecological niche, such as *Sargassum muticum* (Engelen et al. 2008). Thus, *C. humilis* is affected by a series of environmental conditions and human-driven perturbations. In addition, intertidal pools are a highly-fluctuating environment, with sharp contrasts on salinity, pH, temperature, oxygen concentration and water exchange (Teixeira-Roth and Sánchez-Infantas 2006; González-Aragón, 2018), which can influence the distribution of *Cystoseira humilis*.

The thalli of all the tide pools showed a regular distribution ($b < 2$), except for the second tide pool of Bañaderos, which showed an aggregated distribution ($b > 2$). The values of the determination coefficient, which were medium ($R^2 = 0.5$) or low ($R^2 < 0.5$) with the exception of the second tide pool of Bañaderos ($R^2 = 0.82$). The coefficient of determination (R^2) is considered as a pivotal statistical requirement for the definition of patterns, in addition to the significance of the b -values (Giraldo et al. 2002). The R^2 values showed that the distribution pattern is partially fulfilled, so that *Cystoseira humilis* does not fully conform to Taylor's Law.

The identification of scales of variability of macroalgae, including distribution patterns is of utmost importance for implementing monitoring programs and environmental assessment studies (Chapman et al 1995; Veiga et al. 2013). Distribution patterns of algae are pivotal to determine the natural small-scale variation in intertidal and subtidal rocky substrates, and this variation may hide the effects of natural and human-driven perturbations (e.g. Warwick et al. 1988). The lack of thorough information on distribution patterns of macroalgae may lead to erroneous conclusions on the presence or absence of environmental impact on the coastal ecosystem. Thus, the present work constitutes a first approach to pave the path on the distribution patterns of macroalgae; a topic that needs to be further explored by conservationists, stakeholders and even marine ecologists in order to get an accurate picture of the whole coastal ecosystem. This effort needs to be accompanied by the analysis of environmental factors that influence macroalgae distribution such as, temperature, salinity, hydrodynamics, etc.

For future research studies, an increase of sampling effort (number of pools per location, and number of pools) would be an asset, as well as, expanding the study to other islands within the archipelago, and adjacent geographic areas. Lastly, the present study is focused on the spatial variability of the study species, but no temporal replication was conducted. Hence, seasonal variations need to be taken into consideration for future studies. Macroalgae are characterized by a reproductive season along the year, and also may be affected by abrupt and stochastic environmental changes.

ACKNOWLEDGEMENTS

We are grateful to Mr. Antonio Gómez, for the unconditional support and help given throughout this study. Also, to Dr. Francisco Javier Torres Gavilá [Catholic University of Valencia] for his encouragement.

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