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Hierarchical non-linear mixed-effects models for estimating growth parameters of western Mediterranean solitary coral populations

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ABSTRACT

Marine biologists usually assess coral growth through the von Bertalanffy growth function (VBGF), a function of several biological parameters linked to age by a non-linear relationship. Coral growth parameters are then evaluated via ordinary least squares after a linear transformation of the VBGF. Current literature focuses on linearization techniques, but these methods are often used without considering a careful data examination and the presence of variability in coral of the same age or in coral of the same colony. For these reasons, a more thorough approach based on a hierarchical non-linear mixed-effects model is proposed. This model takes into account the influence of sites' characteristics to model heterogeneity between sites. Moreover, the contribution of environmental factors and all the reliable information that may influence coral growth can be suitably modelled. Two model specifications based on the standard and new VBGF parameterizations are introduced to analyse the growth of a solitary coral species *Balanophyllia europaea*. Results from the proposed modelling approach show the importance of including environmental conditions for species coral growth and support; furthermore, the results show the importance of the possibility of accounting for variability from different sources in terms of estimated growth curves.

1. Introduction

In marine biology, demographic parameters of living populations are crucial indicators for investigating the relationships between organisms and their environment and to assess the stability of habitats. In fact, the exploitation of marine resources in fragile ecosystems (coral reefs, coastal bays, and flats of barrier islands) poses some crucial issues for conservation strategies and management purposes. Consequently, marine biologists are very interested in evaluating and monitoring coral growth (Stolarski et al., 2007; Goffredo and Chadwick-Furman, 2000) since the population dynamics of these invertebrates may be considered as an indicator of ecological change and anthropogenic pressure (Ferrigno et al., 2016; Lirman et al., 2014). Individual demographic variables, such as age, oral disk length, and body size, are the basis for modelling the peculiarities of these organisms, as well as the growth and relationships between them and their environment (Ault et al., 2014). It is also relevant to analyse the relationship between coral age and size, as these characteristics are strictly related to reproductive activity that is dependent on how fast corals reach the minimum size to let the planulae exit the oral disk, enabling corals to reproduce. All these considerations highlight the importance of coral growth modelling for the evaluation of habitat stability and provide information on population turnover in order to identify and propose techniques for the restoration of damaged or degraded coastal areas. A popular model used by marine biologists for analysing the growth of several marine organisms (Ricker, 1979; Cailliet et al., 2006; Lloyd-Jones et al., 2014; Purcell et al., 2016) is the von Bertalanffy growth function (VBGF) curve (von Bertalanffy, 1938). This non-linear growth function links the size of fish and invertebrates to their age. Recently, the VBGF has been applied to modelling solitary coral growth in the Mediterranean sea (Goffredo and Lasker, 2008; Goffredo et al., 2010; Caroselli et al., 2012; Cafarelli et al., 2016). There are several methods (hereinafter referred to as traditional methods) for estimating the VBGF parameters (Gulland and Holt, 1959; Fabens, 1965; Basso and Kehr, 1991), however, they are not as accurate as desired (McClanahan et al., 2009) and do not exploit statistical reasoning. The common purpose of the traditional methods is a linear transformation of the VBGF in order to obtain the parameter estimations by ordinary least squares (OLS) (Yee and Barron, 2010). These methods are often applied without considering properties coming from statistical estimation

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theory (Vonesh and Chinchilli, 1997), the statistical distribution of observed data, or the sampling design. In particular, correlation and variability among corals collected at the same site (within-sites) or in different sites (between-sites) is neglected, thus, inducing errors in parameter estimates. Moreover, environmental site specific characteristics related to genetic and environmental factors, such as sea water temperature (Galli et al., 2016), ultraviolet-B radiation, surface ocean acidification, and human anthropogenic stress (Caroselli et al., 2012), cannot be directly inserted in the VGBF. In order to overcome these limitations, we suggest hierarchical nonlinear mixed effects models (HNLMMs) as a more feasible approach to estimate parameters of the von Bertalanffy coral growth function and propose an alternative VBGF parameterization that considers the influence of environmental conditions on the site where individual coral data are collected. Rather than following the growth process of marked individuals over time, we refer to different individuals at the same site to allow the description of species growth (Schaalje et al., 2001). This simplification makes data collection dramatically easier, as is desirable for submarine entities. We first introduce and discuss the two alternative specifications of the VBGF, then we define the HNLMM approach for coral data. Finally, we assess the proposed approach to solitary coral species living in the Mediterranean sea. In particular, we consider *Balanophyllia europaea* since this species has interesting demographic characteristics and peculiar relationships with the environment, which can be used by marine biologists for assessing habitat stability and suitability with regards to climatic changes and human anthropogenic stress (Caroselli et al., 2012; Goffredo and Lasker, 2008; Meesters et al., 2004).

2. Growth models for solitary corals: alternative von Bertalanffy parameterizations

The VBGF is built following the assumption that for each individual, food intake scales with body surface, while the maintenance costs scale with body volume. Starting from the biological proposition that organisms of the same species have a maximum structural length, L_∞, the growth curve of an individual with constant food availability, or any abundance of food, is described by

$$\frac{dL}{dt} = k(L_\infty - L), \tag{1}$$

where k is the growth rate, which is related to maintenance costs, and L is the length at time t. Goffredo et al. (2010) suggested representing corals growth by rewriting (1) as

$$y(t) = L_\infty(1 - e^{-Kt}), \tag{2}$$

where $y(t)$ is the individual length at age t, L_∞ is the asymptotic length representing the maximum theoretical value that a species will tend towards, and K is the constant known as the Brody growth coefficient, i.e., the rate at which growth approaches this asymptote.

Model (2) does not account for the influence of environmental covariates. To this end, in the spirit of Galluci and Quinn (1979), we propose a new parameterization of the VBGF as follows. According to Koojiman (2000), for organisms of the same species with different food availabilities, the logarithm of the VBGF growth rate, K, decreases linearly with the asymptotic length, $ln(k) \propto 1/L_\infty$; thus, different combinations of K and L_∞ can give approximately the same fit (as well as high values of K combined with low values of L_∞ and vice versa). In particular, Kooijman et al. (2008) pointed out that L_∞ can be considered as independent from the environmental conditions, which allows us to consider the following parameterization of (2):

$$y(t) = L_\infty(1 - e^{-te^{\frac{c}{L_\infty}}}), \tag{3}$$

where $c = ln(K)L_\infty$. Following a biological perspective, the new parameter c introduced in (3) can be seen as the part of individual length growth linked to site-specific conditions such as environmental factors. Compared to the traditional specification of the VBGF in (2) and (3) accounts for the global effects of site-specific environmental covariates by means of the new parameter c; consequently, it also obtains a more reliable result in terms of model estimation.

The validity of the proposal of curves such as (2) and (3) is essentially descriptive. Moreover, the curve can be proposed for the growth of an individual, but also holds for aggregated cases if the y values have the meaning of group averages.

3. Different approaches for estimating VBGF parameters

The parameter estimation characterizing the growth of coral populations can be achieved by means of traditional methods or the HNLMMs proposed herein.

3.1. Traditional methods

The methods broadly used for estimating the VBGF parameters are the Gulland-and-Holt (GH) plot (Gulland and Holt, 1959), size-increment method proposed by Fabens (1965), linearization proposed by Basso and Kehr (1991), and the parameterization by Galluci and Quinn (1979). Each method proposes a re-parameterization of (2) in order to obtain linear regression models that use the OLS method to estimate parameters. These methods are easy to implement but imply several limiting hypotheses. First, traditional methods do not take into account the grouped-structure of data collected *in situ*, and consequently, the association usually expressed by the linear correlation among corals sampled at the same site. In this way, the Gauss-Markov uncorrelated residuals hypothesis, required for linear regression models, is violated. Moreover, ignoring data grouped-structure leads to an overall VBGF parameter estimation, common to the entire population, without the possibility for obtaining site-specific estimates. For any association between L_∞ and K, another limitation is not explicitly considering the influence of environmental parameters such as the sea surface temperature, sea current, solar radiation, and the variability at the coral, colony, and site levels. The above limits and the forced linearization required for using traditional methods may lead to a bias in the VBGF parameter estimates.

3.2. HNLMM approach

In order to overcome the previous drawbacks, HNLMMs are a suitable solution. These models are used in a wide range of subject-matter studies, e.g., biological, agricultural, environmental, and medical applications (Paul and Saha, 2007), especially since suitable software is now available. In particular, they are a natural way to analyse grouped, repeated measures, multilevel data, and block designs.

The HNLMM approach may be regarded as a model formulation that can handle data from several individuals linked to common conditions and suitably consider a non-linear response function (Burnett et al., 1995; Cressie et al., 2009). As in the hierarchical linear case, within- and between-individual variations are accommodated within the framework of a two-stage model (Lindstrom and Bates, 1990). More precisely, at the first stage, which models individual (coral) data, the within-site behavior is characterized by a non-linear regression model based on the VBGF, and the within-site covariance structure is specified by modelling the error term distribution. The between-site variability is represented in the second stage through site-specific regression parameters, which also