



Jackknife-corrected parametric bootstrap estimates of growth rates in bivalve mollusks using nearest living relatives



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ABSTRACT

Quantitative estimates of growth rates can augment ecological and paleontological applications of body-size data. However, in contrast to body-size estimates, assessing growth rates is often time-consuming, expensive, or unattainable. Here we use an indirect approach, a jackknife-corrected parametric bootstrap, for efficient approximation of growth rates using nearest living relatives with known age–size relationships. The estimate is developed by (1) collecting a sample of published growth rates of closely related species, (2) calculating the average growth curve using those published age–size relationships, (3) resampling iteratively these empirically known growth curves to estimate the standard errors and confidence bands around the average growth curve, and (4) applying the resulting estimate of uncertainty to bracket age–size relationships of the species of interest. This approach was applied to three monophyletic families (Donacidae, Mactridae, and Semelidae) of mollusk bivalves, a group characterized by indeterministic shell growth, but widely used in ecological, paleontological, and geochemical research. The resulting indirect estimates were tested against two previously published geochemical studies and, in both cases, yielded highly congruent age estimates. In addition, a case study in applied fisheries was used to illustrate the potential of the proposed approach for augmenting aquaculture management practices. The resulting estimates of growth rates place body size data in a constrained temporal context and confidence intervals associated with resampling estimates allow for assessing the statistical uncertainty around derived temporal ranges. The indirect approach should allow for improved evaluation of diverse research questions, from sustainability of industrial shellfish harvesting to climatic interpretations of stable isotope proxies extracted from fossil skeletons.

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1. Introduction

Body size is one of the most fundamental biological variables that can be estimated quantitatively for most organisms, both extant and fossil, using direct measurements. In contrast, comparably fundamental biological parameters – age of individuals and growth rates controlling age–size relationships within populations – are less trivial to estimate. Moreover, because growth rates can be affected by environmental conditions and tend to vary within and across species, determining growth rates for any given population may require new field or laboratory data, even for extant groups for which pre-existing growth rate estimates are available in the literature. Estimating age–size relationships is even more challenging for fossils even if closely related extant species exist. In this paper, we focus on three monophyletic families of bivalves (Donacidae, Mactridae, and Semelidae) to explore an indirect approach for estimating age and growth rates of individuals and populations for which direct field or laboratory data are not available.

In this approach, growth–size relationships are approximated indirectly, by applying a resampling approach to literature-based growth rate estimates reported for populations of nearest living relatives inhabiting comparable environments (i.e. similar temperatures, seasonality, water chemistry, nutrient levels, etc.).

A two-pronged rationale motivates this study. First, estimates of growth rates (both for individuals and populations) have wide applications within biological sciences and beyond. For example, in applied and environmental contexts, from conservation biology to aquaculture industry, even an approximate knowledge of growth rates can help to assess the short-term ecological changes, recovery times from environmental disturbances and pollution, or maximum sustainable yields in food sources (Beverton and Holt, 1957; Chapman, 1961; Saucedo and Monteforte, 1997; Arneri et al., 1998; Gaspar et al., 1999; Melchor-Aragón et al., 2002; Laudien et al., 2003; De Nóbrega and Lessa, 2009). Similarly, in geochemical and paleoclimatologic studies, biomineralized skeletons (e.g., mollusk shells) are sampled along their growth axes to obtain diverse geochemical proxies of various environmental and climatic parameters (Romanek and Grossman, 1989; Ivany et al., 2000; Schöne et al., 2002; Goodwin et al., 2003; Dettman et al., 2004; Carré et al., 2005; Carroll et al., 2006; Riascos, 2006). Such geochemical data

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often represent a spatial series of micro-samples collected along the growth axis of the skeleton. Consequently, an understanding of growth rates of sampled skeletons can be critical when interpreting extracted patterns (e.g., do environmental fluctuations suggested by changes in geochemical proxies record sub-seasonal, multi-seasonal, or multi-decadal records?). Another obvious application of indirect growth rate estimates involves paleontological samples, where growth estimates cannot be measured directly and often can only be inferred using other approaches such as stable isotope sclerochronology (e.g., Steuber, 1996, Kirby et al., 1998), an indirect approach requiring substantial lab work that is often beyond the scope of primary research.

The second rationale for this study is the fact that whereas direct growth estimates are possible in many cases, such substantial data collecting is often not feasible. Admittedly, the indirect method proposed here is much less precise and less accurate than the direct methods applicable to biomineralizing organisms such as notching, tag/recapture, length/frequency population distributions and sclerochronological techniques (see methods in Pearson and Munro, 1991, Mitchell et al., 2000, Melchor-Aragón et al., 2002). These direct approaches are typically major undertakings that are not only time-demanding and field-intensive, but also ecologically invasive. While the approach proposed herein is not meant as a replacement to field study of growth rates, many studies require an understanding of the age of specimens based on size while the growth rates in particular do not represent the primary research target. A key advantage of the proposed approach is that for such studies an indirect estimate will suffice and can be applied when direct measurement techniques are not applicable (e.g., the fossil record). The approach requires only limited data harvesting and analytical time while providing growth rate estimates that may be adequate for many biological, paleontological, and geochemical applications.

Here, we apply indirect estimates to evaluate growth rates of species from three families of marine mollusk bivalves. Indirect estimates of growth rates in bivalve mollusks are particularly feasible because there is a sizable collection of published data available on the growth rates of this taxon, due in large part to the numerous practiced methods of ascertaining age and growth rate as mentioned above. Another reason for the abundance of published bivalve growth rate data is the wide range of fields for which growth estimates are relevant, including marine biology, ecology, paleontology, geochemistry, paleoclimatology and the shellfish industry.

The usefulness and veracity of resulting indirect estimates for the examined bivalve mollusks in this study is then assessed using two published reports on bivalve species for which the geochemical data were collected along the shell growth axis. These two case examples include one species with an unknown growth rate with age estimates acquired using oxygen isotope data and one species where growth rates were known and could be used to independently test the indirect estimates derived here. In addition, we illustrate briefly how indirect growth estimates can augment the fisheries research and inform harvesting and sustainability practices.

2. Indirect resampling approach for estimating growth rates

2.1. Generalized protocol

We propose a four-step protocol for indirectly estimating the growth rate of a specimen (or a monospecific sample of specimens) with unknown age–size relationship using nearest living relatives for which growth rates are available:

1. empirical growth rates reported previously for the same or closely related species (preferably congeneric species) are compiled from the literature. These estimates should represent

comparable environmental settings to those from which the evaluated sample was collected. A maximally exhaustive literature search of all relevant taxa should be conducted (in most cases the number of reported growth curves will be relatively limited and will need to be restricted further to studies reporting the usable growth rate metrics from relevant environmental settings). The resulting dataset provides a sample of empirical growth curves for the nearest living relatives of the species that is being estimated.

2. an average growth curve of the nearest living relatives is computed using some measure of central tendency applied to empirical growth–size data. The growth rate metric used most commonly across the compiled studies should be targeted to maximize the number of usable growth curves and derive maximally robust growth rate estimates. In a case example used below, a parametric approximation (3-parameter von Bertalanffy growth functions) was used to summarize growth curves and compute average curves.
3. a resampling strategy is applied to estimate the standard errors and confidence bands around the average growth curve obtained in Step 2. A parametric bootstrap (based on resampling of von Bertalanffy parameters in this study) is used to estimate an expected sampling distribution of growth curves. In addition, a “leave-one-out” (jackknife-style) correction is applied to the growth curves. By iteratively removing individual populations and comparing the remaining growth curves, this jackknife-style resampling method provides larger error rate estimates. The jackknife correction, by evaluating sequentially each species/population with known growth rates as if it were unknown, generates more conservative and realistic estimates of error when estimating growth rates for an unknown specimen.
4. the jackknife-corrected bootstrap estimates are then applied to the sample of interest to convert size data into age data. We recommend that 2.5th and 97.5th percentiles of jackknife-corrected sampling distributions be applied to estimate growth rate uncertainties for the specimen(s) of interest. The standard error of the estimate would also be an applicable (if less conservative) strategy for assessing errors around the growth rate estimates.

The proposed four-step protocol assumes that the empirically estimated growth rates of nearest living relatives and the unknown growth rates of the species of interest came from the same underlying population of possible growth rates. In practice, the generalized protocol outlined above will vary in detail when applied to specific datasets. In particular, decisions have to be made regarding: (1) the method of measuring growth rates; (2) an appropriate estimate of central tendency; and (3) practical details of resampling procedure. Below, we discuss those decisions in the context of mollusk bivalves characterized by accretionary skeletons and indeterminate growth.

Following the analysis, post-hoc evaluations of resulting indirect estimates are recommended, including sensitivity analyses and cross-testing against empirical case studies (example of such post-hoc evaluations are illustrated later in this report).

2.2. Measuring growth rates

Whereas direct empirical curves can be generated in many cases to describe the relation between age and size of specimens, researchers frequently use parametric approximations (or growth functions) that provide a continuous representation of growth rates and can be summarized in terms of a few parameters. These parametric measures of growth rates are often reported in individual studies and facilitate comparisons across studies (especially when considering that empirical methods of deriving growth rates vary across studies even for closely related taxa). Also, the parametric functions provide an attractive system for developing statistical estimates of growth rates, as outlined in our 4-step protocol above.

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