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A Matrix Population Model for Growth of the Echinoid Skeleton

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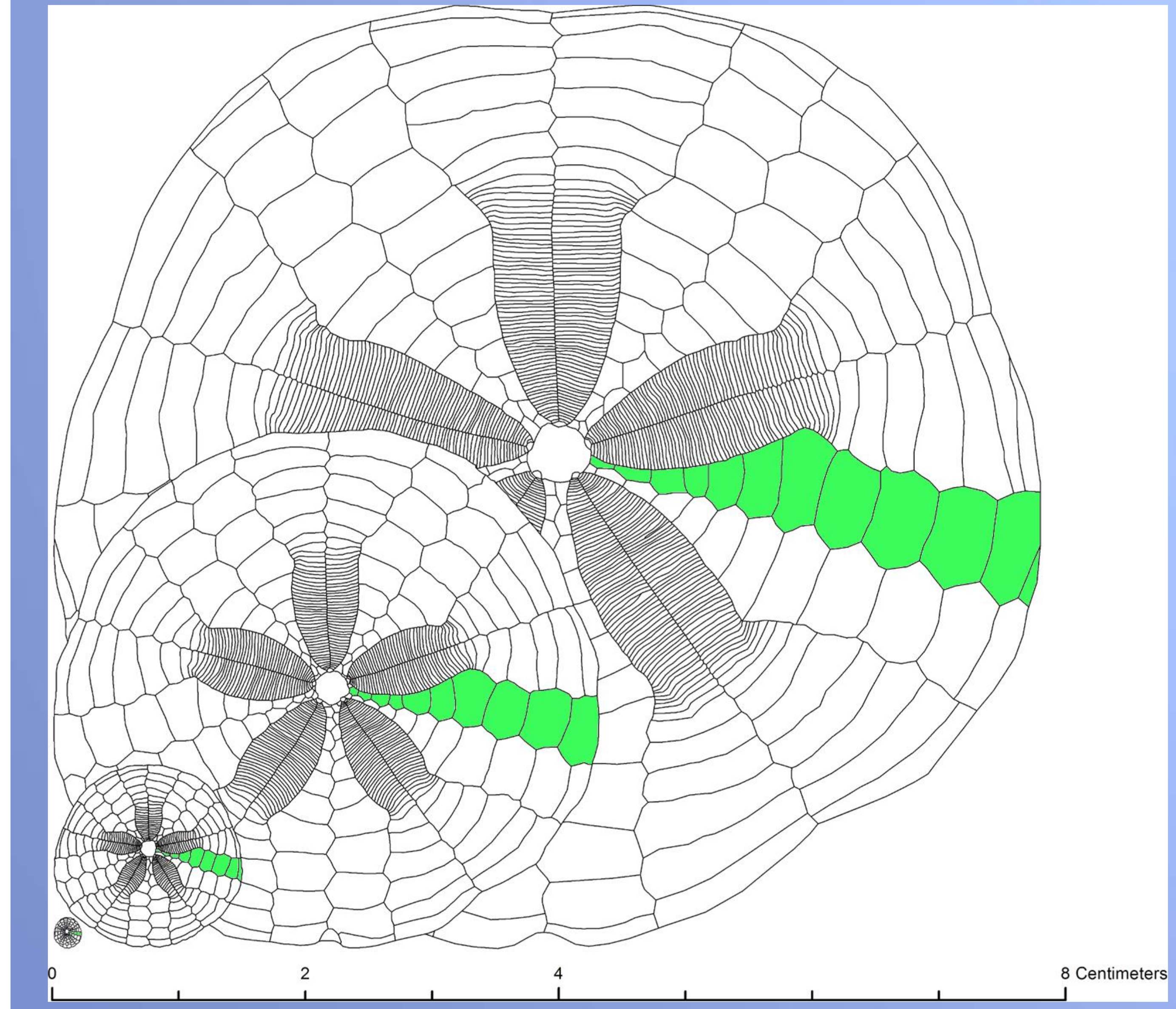
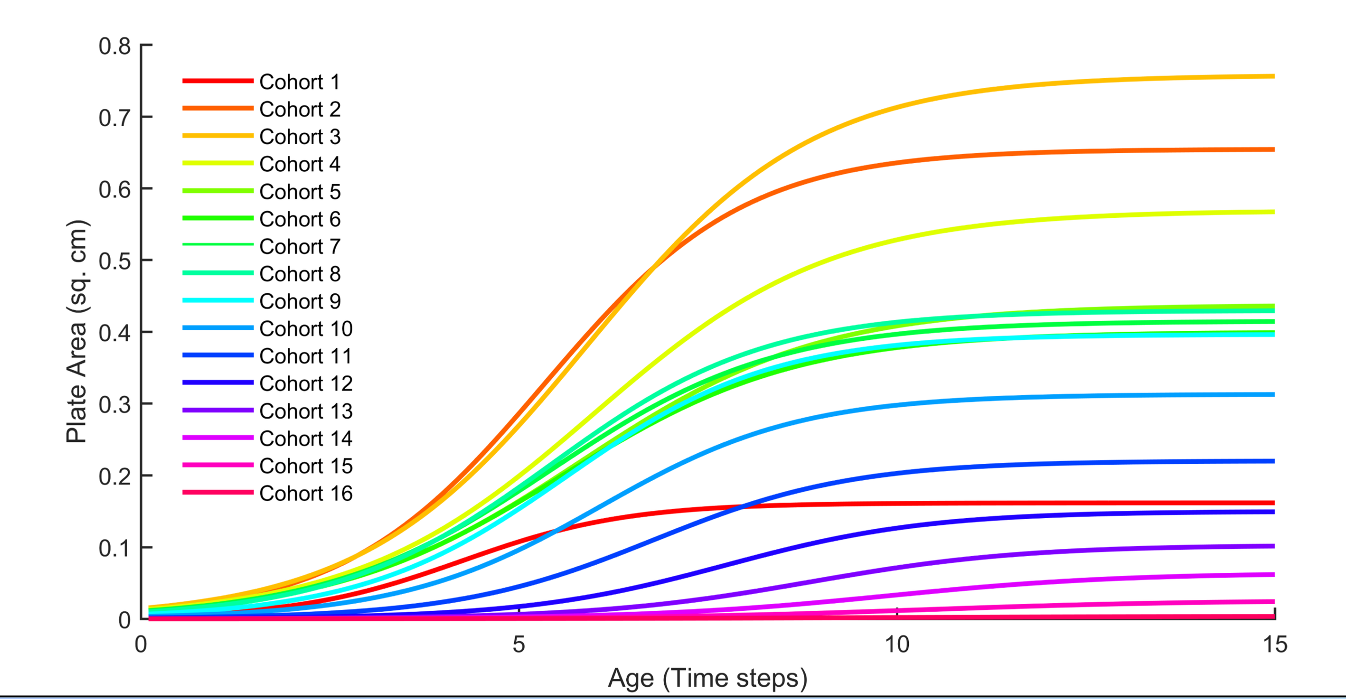
Abstract

The skeleton of an echinoid comprises hundreds to thousands of individual calcite plates. The collection of plates is analogous to a population of organisms. Traditional structured population models in biology treat populations of organisms as individuals (or cohorts of individuals) with specific birth and death rates that lead to stable age distributions. The simplest models can be represented as Leslie projection matrices, based on age-specific survivability and fecundity rates. The conceptual leap to representation of the echinoid skeleton as a population of plates is aided by consideration of a life cycle graph. For example, take a stylized life cycle graph of a single column of plates in a sea urchin test, representing each growth stage with a subscripted C_i, where C_1 represents the first cohort of plates with an inherent fecundity of 0. Growth of new plates (fecundity) is density dependent. A realistic system will reach a stable plate size distribution representing a plate column of an adult urchin. A complete representation must take into account the fact that growth in urchins proceeds not by a single column, but in column pairs of alternating plates. Additionally, growth differs between ambulacral paired columns and interambulacral paired columns. Multiple interdependent life cycle graphs are needed to represent growth, requiring multi-dimensional population matrices and tensor algebra to calculate solutions. Geometric models derived from the plate population matrices are developed on functional surfaces representing gross morphology of various echinoid classes and families, using Voronoi polygonalization to constrain plate morphology. Models can be validated from 3-dimensional plate configurations derived from computed tomography of actual echinoid skeletons. Results indicate that phylogenetically significant characters can be mathematically derived from the parametric structure of the plate population matrices. It is the nature of such parametric models that under certain conditions the models becomes unstable, becoming unbound or oscillating between two or more attractors. Failure in these cases to converge to stable growth configurations could explain why much of the theoretical morphospace of echinoids is unrealized in nature.

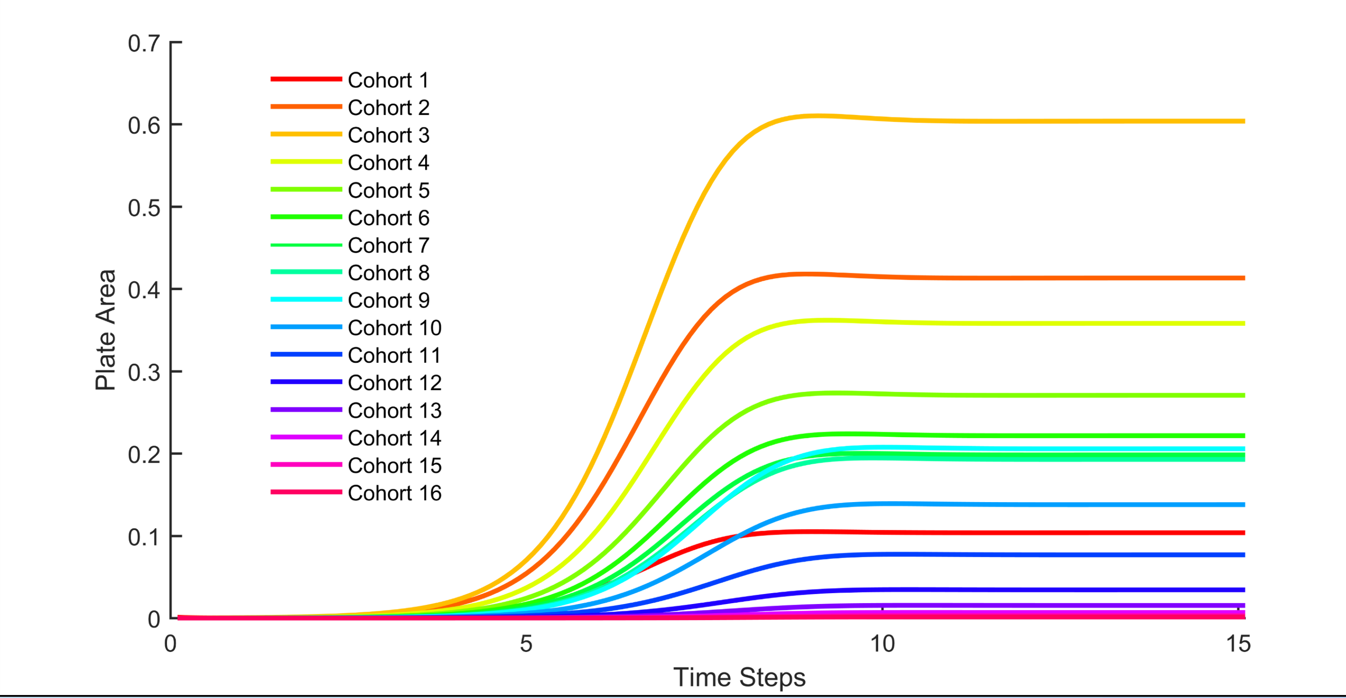


Echinarachnius parma
Interambulacral column in green



Actual Growth

Modeled Growth



1. Overall somatic growth of an echinoid can be represented by the Bertalanffy growth function (Bertalanffy, 1938), but it has been shown that individual plate growth is more closely modeled by the logistic function (Zachos, 2009, 2015), of which the Bertalanffy function is a special case.

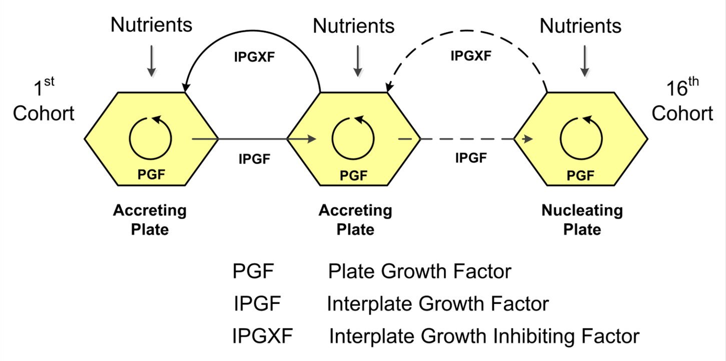
2. Growth curves for *E. parma* are modeled on logistic parameters which are based on actual plate measurements (Zachos, 2015). Parametric values averaged from all 10 interambulacral columns across16 cohorts .

Logistic Growth Curve Parameters
Echinarachnius parma

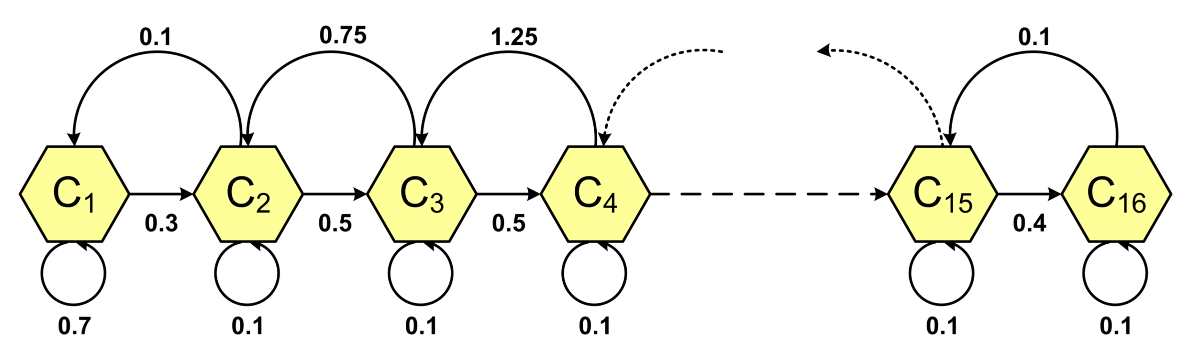
Interambulacra

Plate Cohort	K	r	t_0
1	0.161550	0.091168	42.478217
2	0.654406	0.075213	53.368327
3	0.757713	0.067083	58.867788
4	0.568934	0.063597	59.766596
5	0.437131	0.063091	58.091608
6	0.399704	0.064560	55.790467
7	0.414876	0.067256	54.224935
8	0.429707	0.070493	54.220937
9	0.396455	0.073562	56.284526
10	0.312913	0.075725	60.761912
11	0.220144	0.076288	67.850765
12	0.149778	0.074716	77.404520
13	0.102644	0.070761	88.485701
14	0.063964	0.064539	98.749388
15	0.025807	0.056532	104.115342
16	0.003608	0.047484	99.709475

K: Maximum size
r: Maximum growth rate
t_0: Time at midpoint



Conceptual Model



Life-Cycle Graph

0.70	**0.10**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.30	**0.10**	**0.75**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	**0.50**	**0.10**	**1.25**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	**0.50**	**0.10**	**0.10**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	**0.60**	**0.20**	**0.01**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	**0.65**	**0.20**	**0.10**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	**0.70**	**0.20**	**0.10**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	**0.80**	**0.20**	**0.10**	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	**0.60**	**0.20**	**0.10**	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**0.50**	**0.10**	**0.01**	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**0.40**	**0.10**	**0.01**	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**0.40**	**0.10**	**0.01**	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**0.40**	**0.10**	**0.01**	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**0.40**	**0.10**	**0.01**	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**0.40**	**0.10**	**0.01**
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**0.40**	**0.10**

Projection Matrix

3. Projection matrix generated by inverse modeling of *E. parma* growth measurements. A conceptual model (which is greatly simplified and purely hypothetical) is used to define a life-cycle graph based on analogy with matrix population models. The life-cycle graph in turn forms the basis for the Leslie matrix (Leslie, 1945, 1948), with the following correspondences:

Inherent plate growth is modeled as an plate growth factor (PGF).

Interplate growth induction is modeled as an interplate growth factor (IPGF).

An interplate growth inhibiting factor (IPGXF), represented as a density dependent parameter $g(N)$, where N is the total size of all plates, and $g(N)$ takes the form:

$$g(N) = e^{-bN}$$

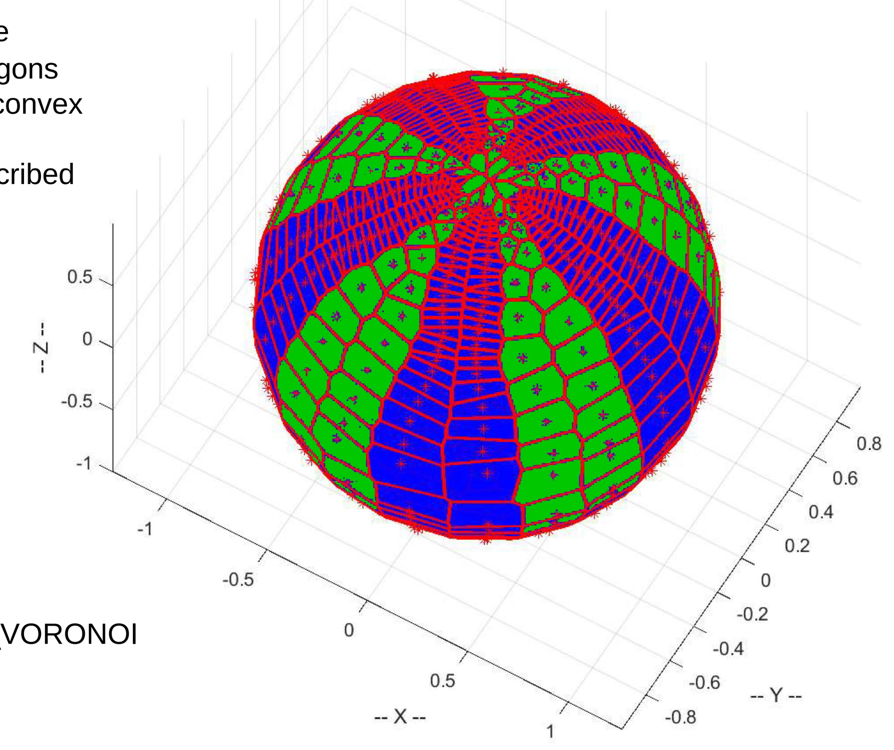
and the corresponding value in the projection matrix is a multiplier.

```
% Example MATLAB script
% Implementation of Matrix Population Model
%  for parameters derived from interambulacral
%  E. parma plate averaged logistic growth

% Projection matrix (as a sparse matrix)
A = diag([.7 .1 .1 .1 .2 .2 .2 .2 .2 .1 .1 ...
    .1 .1 .1 .1 .1]);
B = [.3 .5 .5 .6 .6 .65 .7 .8 .6 .5 .4 .4 ...
    .4 .4 .4 0; 0 .1 .75 1.25 .1 .01 .1 .1 ...
    .1 .1 .01 .01 .01 .01 .01 .01 ]';
d = [-1 1]';
A = spdiags(B,d,A);

%Initial plate sizes
n = [.001;0;0;0;0;0;0;0;0;0;0;0;0;0;0;0];

b = .1;
g = ones(16,16);
%Calculate plate growth for given time steps
for ts = 1:150
    N = sum(n(:,ts));
    fg = exp(-b*N);
    for x = 1:15
        g(x,x+1) = fg;
    end
    n = [n (A.*g)*n(:,end)];
end
```

4. Because the iterative processing uses matrix algebra, implementation in MATLAB is straight-forward.

Visualization

5. Modeling results can be displayed as Voronoi polygons mapped over a spherical convex hull of plate centerpoints, following conventions described by Zachos (2009)



Visualization using MATLAB Library SPHERE_VORONOI
GNU LGPL License
John Burkhardt 2015

Preliminary Results

6. This study is still in an early stage of development. These results are meant to show a proof of concept that the tools developed from matrix population models (Caswell, 2001; Cushing, 1998) are applicable to the problem of describing growth in the modular tests of echinoids. Realistic models incorporating the full heterogeneity of an echinoid test will require combined models analogous to age x stage-classified analysis (Caswell et al., 2018) and/or hyperstate matrix models incorporating multiple feedback loops (Roth et al., 2016).

References

BERTALANFFY, L. V. 1938. A quantitative theory of organic growth (inquiries on growth laws. II). Human Biology, 10(2):181-213.
CASWELL, H. 2001. Matrix Population Models, Construction, Analysis, and Interpretation. Sinauer Associates, Sunderland, MA, 2nd edition, 722 p.
CASWELL, H., C. DE VRIES, N. HARTEMINK, G. ROTH, S. F. VAN DAALEN. 2018. Age X stage-classified demographic analysis: a comprehensive approach. Ecological Monographs, https://doi.org/10.1002/ecm.1306, 25 p.
CUSHING, J. M. 1998. An Introduction to Structured Population Dynamics. Society for Industrial and Applied Mathematics, Philadelphia, 71, 193 p.
LESLIE, P. H. 1945. On the use of matrices in certain population mathematics. Biometrika, 33(3):183-212.
LESLIE, P. H. 1948. Some further notes on the use of matrices in population mathematics. Biometrika, 35(3/4):213-245.
ROTH, G., H. CASWELL, M. REES. 2016. Hyperstate matrix models: extending demographic state spaces to higher dimensions, Methods in Ecology and Evolution, 7(12):1438-1450.
ZACHOS, L. G. 2009. A new computational growth model for sea urchin skeletons. Journal of Theoretical Biology, 259(3):646-657.
ZACHOS, L. G. 2015. Holistic morphometric analysis of growth of the sand dollar *Echinarachnius parma* (Echinodermata:Echinoidea:Clypeasteroida). Zootaxa, 4052(2):151-179