

Budding Yeast, Branching Processes, and Generalized Fibonacci Numbers

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The Fibonacci sequence is famous for showing up in nature in many ways, some of them idealized (like Fibonacci's breeding rabbits) and some very practical. In this article we describe an application of a generalization of the Fibonacci sequence, called the " k -nacci numbers." In Olofsson and Bertuch [6], a branching process model was used to analyze experiments on growing yeast populations, and it turned out that the k -nacci numbers were crucial to practical results and calculations. That paper mainly addressed the biological problems. Our aim in this article is to elaborate on some of the mathematics involved, and in so doing, to give a nice example of how asymptotic results about simple recurrences can be of significant practical use.

Budding yeast

The yeast *Saccharomyces cerevisiae* is used in baking and brewing, and is also one of the most important model organisms in biology. It is a one-celled organism that reproduces through *budding*, meaning that a new yeast cell starts to grow on the surface of an existing cell, eventually separating from its mother as a newborn daughter cell. This reproduction scheme is different from *binary fission*, common in many bacteria such as *E. Coli*, where the cell divides into two new cells of equal size. Although both reproduction schemes give rise to *clones*, that is, cells that are genetically identical (save for mutations), there are differences that matter to the mathematical modeling of the resulting population growth.

Since yeast has linear chromosomes just like human beings, its genetics can be studied for greater insight into human genetics. One example is the study of the shortening of chromosomal ends known as *telomeres* that occurs also in many of our cells. With each cell division, telomeres become progressively shorter until they reach a point at which the cell stops dividing, to avoid damage to the coding DNA in the interior of the chromosome. A cell that has stopped dividing is said to be *senescent*. To counteract telomere shortening, some cells, for example embryonic stem cells, contain the enzyme *telomerase* which adds telomere sequences so that the chromosomes can maintain a stable telomere length. Some cells manage to keep replicating even without telomerase; such populations were studied in Olofsson and Bertuch, who used branching processes to model populations of yeast cells and to estimate cell population parameters from laboratory data.

Branching processes

A branching process is a stochastic model for a proliferating population. Assumptions are made about individual cell lifetimes and reproduction patterns, and conclusions are drawn about population behavior. In this section we introduce a branching process that applies to cells (such as *E. Coli*) that use binary splitting. We then show how it can be modified to apply to cells (such as yeast) that reproduce by budding.

We begin with a single ancestral cell, which we call *generation 0*. Then, for $n \geq 0$, each cell in generation n divides into two cells in generation $n + 1$. Randomness enters via the cell lifetimes (birth to division). These are random variables, independent and identically distributed, with a common cumulative distribution function (cdf) F . That is, if T is a cell lifetime, then

$$\Pr(T \leq t) = F(t) \text{ for all } t \geq 0.$$

In general, if two independent random variables have cdf's F and G , then the cdf of their sum is the *convolution* of F and G , defined by

$$(F * G)(t) = \int_{s=0}^t G(t-s) dF(s) \text{ for all } t \geq 0.$$

(If F has a derivative, one may read “ $dF(t)$ ” as a synonym for $F'(t)dt$.) Therefore, if F is the cdf for cell lifetimes, the sum of n consecutive cell lifetimes has cdf equal to the n -fold convolution of F with itself, which we denote by F^{*n} .

We would like to derive an expression for $M(t)$, the expected number of individuals present at time t . First note that there are 2^n cells in the n th generation. Such a cell is present at time t if the sum of n cell lifetimes (those of its ancestors) is less than t and the sum of $n + 1$ cell lifetimes (its ancestors and itself) is greater than t . Thus, the probability that an n th-generation cell is present at time t equals $F^{*n}(t) - F^{*(n+1)}(t)$ and the expected number of cells in generation n that are present at time t equals

$$2^n (F^{*n}(t) - F^{*(n+1)}(t)).$$

This formula applies to generation 0 as well, if we follow the usual convention that $F^{*0}(t) = 1$. Now, summing over all generations gives the expression

$$M(t) = \sum_{n=0}^{\infty} 2^n (F^{*n}(t) - F^{*(n+1)}(t)). \quad (1)$$

So far, we have assumed that all cells survive to reproduce. If we instead assume that each cell survives to reproduce with probability p , and otherwise dies (after its random lifetime) without reproducing, then the mean number of offspring per cell is $m = 2p$. We always assume that $p > 1/2$, so that $m > 1$ and the generations (on average) increase in size. Now, in place of (1) we get the expression

$$M(t) = \sum_{n=0}^{\infty} m^n (F^{*n}(t) - F^{*(n+1)}(t)). \quad (2)$$

Adopt the standard notation $x(t) \sim y(t)$ if $x(t)/y(t) \rightarrow 1$ as $t \rightarrow \infty$. It turns out that the asymptotic growth rate of $M(t)$ is given by

$$M(t) \sim be^{\alpha t} \text{ as } t \rightarrow \infty \quad (3)$$

where the constants α and b are determined by the lifetime cdf F and the mean number of offspring per individual m . Specifically, let

$$\widehat{F}(s) = \int_0^\infty e^{-st} dF(t)$$

the Laplace transform of the probability measure associated with F . The growth rate α , called the *Malthusian parameter*, is defined through the relation

$$m\widehat{F}(\alpha) = 1$$

where $m > 1$ implies that there exists a unique solution $\alpha > 0$. The constant b can be shown to equal

$$b = (m - 1) \left(\alpha m^2 \int_0^\infty t e^{-\alpha t} dF(t) \right)^{-1}.$$

We refer to Chapter VI in Harris [4] or Jagers and Nerman [5] for proofs and further details.

Yeast, as we have noted, does not reproduce by binary splitting but rather by budding. Each cell in generation n still gives rise to two cells, and although one is the mother and the other is the daughter, after the division we still refer to both of them as generation $n + 1$. In this sense there is no difference from binary splitting; but it is known that a mother cannot give birth to an unlimited number of daughters, so the size of the n th generation is no longer given by m^n .

We can still obtain a formula for $M(t)$, if we let $m(n)$ represent the number of cells in the n th generation. We then have, for yeast,

$$M(t) = \sum_{n=0}^\infty m(n) (F^{*n}(t) - F^{*(n+1)}(t)). \tag{4}$$

Growth rate and other asymptotic properties of $M(t)$ are now determined by F together with $m(n)$. Everything depends on getting a handle on the numbers $m(n)$. We address this task in the next section.

Generalized Fibonacci numbers

By the k -nacci sequence, for $k \geq 2$, we mean the sequence $\{F_j, j \geq 0\}$ defined by $F_0 = F_1 = \dots = F_{k-2} = 0, F_{k-1} = 1$, and $F_n = F_{n-1} + F_{n-2} + \dots + F_{n-k}$ for $n \geq k$. For example, when $k = 4$, each term is the sum of the four previous terms:

$$0, 0, 0, 1, 1, 2, 4, 8, 15, 29, 56, \dots$$

In the yeast population, suppose that a mother cell can have k daughter cells before she stops reproducing. (In biology, k is known as the *proliferative lifespan*.) In any given generation n , cells can be divided into classes describing how many more daughter cells they can have. Thus, let $N_j^{(n)}$ be the number of cells in generation n that can have exactly j additional daughter cells for $j = 0, 1, \dots, k$. The class with $j = 0$ is the class of senescent cells, and we assume that they stay in the population indefinitely (although it is easy to model a scenario where they eventually die and disappear). The class with $j = k$ are the newborn cells that have yet to reproduce. As it turns out, the numbers of cells in these classes are precisely described by the k -nacci sequence.

PROPOSITION 1. Consider the vector $(N_0^{(n)}, N_1^{(n)}, \dots, N_k^{(n)})$ in the n th generation for $n \geq 1$ of the branching process above. Let F_i denote the i th k -nacci number and let $S_n = F_0 + F_1 + \dots + F_n$. Then $(N_0^{(n)}, N_1^{(n)}, \dots, N_k^{(n)})$ equals

$$(S_{n-1}, F_n, F_{n+1}, \dots, F_{n+k-1}).$$

Proof. In generation 0 there is one cell that is able to divide k more times which gives the vector $(0, 0, \dots, 0, 1)$ for generation 0. Each cell with $j \geq 1$ produces a daughter cell that is able to reproduce k times and is then itself able to reproduce another $j - 1$ times. Cells with $j = 0$ remain unchanged. Thus, each class with $j \geq 1$ feeds into the class $j - 1$ immediately below it, and also into the highest class k . The transition from generation $n - 1$ to generation n can be described as follows:

$$\begin{cases} N_0^{(n)} = N_0^{(n-1)} + N_1^{(n-1)} \\ N_{j-1}^{(n)} = N_j^{(n-1)} \text{ for } 2 \leq j \leq k \\ N_k^{(n)} = \sum_{j=1}^k N_j^{(n-1)} \end{cases}$$

and the proposition follows. ■

The total number, $m(n)$, of cells in the n th generation equals

$$\begin{aligned} m(n) &= S_{n-1} + F_n + \dots + F_{n+k-1} \\ &= S_{n+k-1} \end{aligned}$$

and Proposition 1 provides a recursive scheme that enables us to compute $m(n)$. For example, if $k = 4$, the first terms in the sequence $\{m(n), n \geq 0\}$ are

$$1, 2, 4, 8, 16, 31, 60, 116, 224, \dots$$

where we recognize the powers of 2 until the 4th generation ($n = 4$) after which the effect of the proliferative lifespan $k = 4$ becomes noticeable and slows down the growth. By (4), we can also compute the expected number $M(t)$ of cells at each time t which enables us to compare the model with laboratory data and estimate unknown parameters. As it turns out, we can even get an explicit expression for $m(n)$, expressed in terms of k -nacci numbers which is crucial to establish asymptotics of the branching process.

In the next section, we study the k -nacci numbers as a special case of linear recurrence.

Linear recurrences

Given a positive integer k and complex numbers $a_0 \neq 0, a_1, \dots, a_{k-1}$ consider a sequence $\{R_n\}_{n=0}^\infty$ that satisfies the k -term linear recurrence

$$R_n = a_{k-1}R_{n-1} + a_{k-2}R_{n-2} + \dots + a_0R_{n-k} \tag{5}$$

for all $n \geq k$. Given initial values R_0, R_1, \dots, R_{k-1} , equation (5) defines the sequence $\{R_n\}_{n=0}^\infty$ recursively. Define the *characteristic polynomial* of (5) to be

$$p(x) = x^k - a_{k-1}x^{k-1} - a_{k-2}x^{k-2} - \dots - a_0. \tag{6}$$

If the polynomial (6) has k distinct roots r_1, r_2, \dots, r_k then there are unique complex coefficients b_1, b_2, \dots, b_k so that

$$R_n = b_1r_1^n + b_2r_2^n + \dots + b_kr_k^n \tag{7}$$

for all $n \geq 0$. The coefficients b_1, \dots, b_k can be computed from the initial values R_0, \dots, R_{k-1} . For details, and for the case of repeated roots, see Elaydi [1, Section 2.3].

Given a sequence $\{R_n\}_{n=0}^\infty$ that satisfies (5), we let $S_n = R_0 + R_1 + \dots + R_n$ for $n \geq 0$. The following proposition establishes a closed form expression for S_n .

PROPOSITION 2. *Consider the linear recurrence in (5). Assume that the characteristic polynomial has k distinct roots, none of which equals 1. Then there exist constants c_0, \dots, c_{k-1} such that*

$$S_n = \sum_{l=0}^{k-1} c_l R_{n+l+1} - \sum_{l=0}^{k-1} c_l R_l.$$

Proof. Begin by expressing R_n as given in (7). Then we have

$$\begin{aligned} S_n &= \sum_{i=0}^n R_i \\ &= \sum_{i=0}^n \sum_{j=1}^k b_j r_j^i \\ &= \sum_{j=1}^k b_j \sum_{i=0}^n r_j^i \\ &= \sum_{j=1}^k b_j \frac{r_j^{n+1} - 1}{r_j - 1}. \end{aligned}$$

Since the characteristic polynomial $p(x)$ does not have 1 as a root, $p(x)$ and $x - 1$ are relatively prime so that we can find polynomials $u(x)$ and $v(x)$ which satisfy

$$v(x)p(x) + u(x)(x - 1) = 1. \tag{8}$$

Moreover, by using the division algorithm if necessary, we can assume that the degree of $u(x)$ is less than k . Substituting any of the roots r_j of $p(x)$ into (8) immediately yields

$$\frac{1}{r_j - 1} = u(r_j).$$

It now follows that

$$S_n = \sum_{j=1}^k b_j (r_j^{n+1} - 1) u(r_j).$$

If we write $u(x) = c_{k-1}x^{k-1} + \dots + c_0$, this becomes

$$\begin{aligned}
 S_n &= \sum_{l=0}^{k-1} c_l \sum_{j=1}^k b_j (r_j^{n+l+1} - r_j^l) \\
 &= \sum_{l=0}^{k-1} c_l (R_{n+l+1} - R_l) \\
 &= \sum_{l=0}^{k-1} c_l R_{n+l+1} - \sum_{l=0}^{k-1} c_l R_l.
 \end{aligned} \tag{9}$$

which concludes the proof. ■

In the expression for S_n , note that the first sum includes at most k terms of the sequence $\{R_n\}_{n=0}^\infty$, while the second sum depends only on the initial conditions R_0, R_1, \dots, R_{k-1} .

As an example, we apply this result to the Fibonacci numbers, which are simply the $k = 2$ case of the k -nacci numbers. The characteristic polynomial in this case is $p(x) = x^2 - x - 1$, which satisfies $-p(x) + x(x - 1) = 1$. Hence, $u(x) = x$ so that Proposition 2 becomes the familiar result $F_1 + F_2 + \dots + F_n = F_{n+2} - F_1 = F_{n+2} - 1$.

As a corollary we obtain the corresponding result for the k -nacci numbers.

COROLLARY 3. *For the k -nacci sequence $\{F_j, j \geq 0\}$, let $S_n = F_0 + F_1 + \dots + F_n$. Then*

$$S_n = \frac{1}{k-1} \left(F_{n+k} - \sum_{l=0}^{k-3} (k-l-2) F_{n+l+1} - 1 \right).$$

Proof. To get an expression for the polynomial $u(x)$ which determines the coefficients c_l in Proposition 2, note that for $k \geq 2$ we have

$$\begin{aligned}
 1 &= \frac{-1}{k-1} (x^k - x^{k-1} - x^{k-2} - \dots - 1) \\
 &\quad + \frac{1}{k-1} (x^{k-1} - x^{k-3} - 2x^{k-4} - 3x^{k-5} - \dots - (k-2)(x-1))
 \end{aligned}$$

which identifies $u(x)$ as

$$u(x) = \frac{1}{k-1} \left(x^{k-1} - \sum_{l=0}^{k-3} (k-l-2)x^l \right),$$

provided we treat the sum as empty when $k = 2$. Clearly the characteristic polynomial $p(x) = x^k - (x^{k-1} + x^{k-2} + \dots + 1)$ does not have 1 as a root. Regarding the distinctness of the roots of $p(x)$, observe that

$$\begin{aligned}
 p(x) &= x^k - \frac{x^k - 1}{x - 1} \\
 &= \frac{x^{k+1} - 2x^k + 1}{x - 1}
 \end{aligned} \tag{10}$$

and the polynomial in the numerator has no repeated roots, as it does not share any roots with its derivative (see Gallian [3]). Finally, since $F_0 = F_1 = \dots = F_{k-2} = 0$ and $F_{k-1} = 1$, the result follows from Proposition 2. ■

Asymptotics of the branching process

The asymptotic results in this section rely on the fact that k -nacci numbers have asymptotic geometric growth. Following Flores [2], there exist numbers r and A such that

$$F_j \sim Ar^j \tag{11}$$

as $j \rightarrow \infty$, meaning that $F_j/r^j \rightarrow A$ as $j \rightarrow \infty$. (This result follows from (7).) The number r is the dominant root of the characteristic equation

$$x^k - x^{k-1} - \dots - x - 1 = 0$$

(that is, the root with the largest absolute value) and it is known to be real and to lie between the golden ratio $\phi \approx 1.618$ and 2. In fact, for $k = 2$, $r = \phi$ and as $k \rightarrow \infty$, $r \uparrow 2$. The constant A equals

$$A = \frac{r - 1}{(k + 1)r^k - 2kr^{k-1}} \tag{12}$$

By Proposition 1, Corollary 3, and (11), we can establish expressions for the asymptotic composition of cells in the different classes, recalling that class j contains cells that can have j additional daughter cells, $j = 0, 1, \dots, k$. Of particular practical interest is the proportion of cells in the 0-class and we state its simple asymptotic expression.

PROPOSITION 4. *Let r be as above. The asymptotic proportion of cells in the 0-class as $n \rightarrow \infty$ equals r^{-k} .*

Proof. By Proposition 1, the proportion equals

$$\frac{S_{n-1}}{S_{n+k-1}}$$

and the proposition follows from Corollary 3 and (11). ■

Proposition 4 is not just a theoretical limit result; it has important practical implications for the yeast cell population studies. Certain computational expressions become greatly simplified if the finite proliferative lifespan can be neglected, i.e., if we assume that each cell can produce an unlimited number of daughter cells. Since the fraction of senescent cells in a given generation n is roughly r^{-k} , this number can be used to justify such an approximation. For example, for the regular Fibonacci sequence with $k = 2$, we have $r = \phi$ and since $\phi^{-2} \approx 0.38$, as many as 38% of cells have reached the end of their proliferative lifespan and are no longer able to produce daughter cells. In this case, the approximation would not work very well. Note that, since $r \uparrow 2$ as $k \rightarrow \infty$, the “ ∞ -nacci” sequence has $r = 2$ and corresponds to a binary splitting branching process where each individual can produce an unlimited number of offspring.

For yeast cells, the proliferative lifespan k has been estimated to be on average 25, Sinclair et al. [7], which gives a value of r that for all practical purposes equals 2 and the fraction of senescent cells is less than one in 10 million. For any reasonable duration of a yeast cell experiment, this fraction is negligible although it does of course

matter to the theoretical asymptotic limits. Calculations show that r exceeds 1.99 already for $k = 7$ in which case less than 1% of cells are senescent. For the particular yeast populations studied by Olofsson and Bertuch, k is likely to largely exceed 7 and the approximation works well.

Finally, we obtain the asymptotic growth rate of $M(t)$. As we will soon show, $m(n)$ grows asymptotically as r^n , that is, at the same rate as a binary splitting process with mean number of offspring equal to $m = r$. Since $m = 2p$, in the latter process each cell survives to reproduce with probability $p = r/2$, and dies without reproducing with probability $1 - r/2$. The next result shows that the Malthusian parameter is the same for the budding process with generation sizes $m(n)$ and the binary splitting process with mean r , but that the budding process always has a larger expected value.

PROPOSITION 5. *As $t \rightarrow \infty$, $M(t) \sim Cbe^{\alpha t}$ where α and b are as in (3) with mean number of offspring $m = r$. The constant C depends on k and satisfies $C > 1$ and $C \rightarrow 1$ as $k \rightarrow \infty$.*

Proof. Since $m(n) = S_{n+k-1}$, Corollary 3 and (11) yield

$$m(n) \sim Cr^n$$

where

$$C = \frac{A}{k-1} \left(r^{2k-1} - \sum_{l=0}^{k-3} (k-l-2)r^{k+l} \right) \tag{13}$$

A being the constant defined in (12). If we, informally, substitute this expression for $m(n)$ in (4), we get

$$M(t) \sim C \sum_n r^n (F^{*n}(t) - F^{*(n+1)}(t)) \tag{14}$$

as $t \rightarrow \infty$. By (2) and (3), we get

$$M(t) \sim Cbe^{\alpha t}$$

as $t \rightarrow \infty$, as desired.

To prove that the substitution leading to (14) is indeed legitimate, let us formally prove that

$$e^{-\alpha t} M(t) \rightarrow Cb$$

as $t \rightarrow \infty$. Recall that $m(n) \sim Cr^n$, that is, $m(n)/r^n \rightarrow C$ as $n \rightarrow \infty$. Choose N such that

$$C - \epsilon \leq \frac{m(n)}{r^n} \leq C + \epsilon$$

for $n > N$. For ease of notation, let

$$P(n, t) = F^{*n}(t) - F^{*(n+1)}(t)$$

for $n = 0, 1, 2, \dots$, and note that $0 \leq P(n, t) \leq 1$ for all n and t . We now get

$$\begin{aligned} e^{-\alpha t} M(t) &= e^{-\alpha t} \sum_{n=0}^{\infty} m(n) P(n, t) \\ &= e^{-\alpha t} \sum_{n=0}^N m(n) P(n, t) + e^{-\alpha t} \sum_{n=N+1}^{\infty} m(n) P(n, t) \end{aligned}$$

where the first term goes to 0 as $t \rightarrow \infty$ and hence the limit of $e^{-\alpha t} M(t)$ is the same as that of the second term, for which we have

$$(C - \epsilon)e^{-\alpha t} \sum_{n=N+1}^{\infty} r^n P(n, t) \leq e^{-\alpha t} \sum_{n=N+1}^{\infty} m(n) P(n, t) \leq (C + \epsilon)e^{-\alpha t} \sum_{n=N+1}^{\infty} r^n P(n, t)$$

Let $t \rightarrow \infty$ and use (3) to obtain

$$(C - \epsilon)b \leq \lim_{t \rightarrow \infty} e^{-\alpha t} M(t) \leq (C + \epsilon)b$$

Since ϵ was arbitrary, we conclude that

$$\lim_{t \rightarrow \infty} e^{-\alpha t} M(t) = Cb$$

To prove that $C > 1$, first note that by (12) and some algebra the constant

$$C = \frac{A}{k-1} \left(r^{2k-1} - \sum_{l=0}^{k-3} (k-l-2)r^{k+l} \right)$$

simplifies to

$$C = \frac{r(r^{k+1} - 2r^k + kr - k - r + 2)}{(r-1)(kr + r - 2k)(k-1)}$$

From (10) we see that

$$r^{k+1} - 2r^k + 1 = 0$$

which simplifies C further, to

$$C = \frac{r}{k(r-2) + r}$$

and since $k \geq 2$ and $\phi \leq r < 2$, we have $C > 1$. Further, (10) yields

$$r^{k+1} - 2x^r + 1 = 0$$

and since $\phi \leq r < 2$, we get the inequalities

$$2 - \phi^{-k} \leq r < 2$$

which reveals that $C \rightarrow 1$ as $k \rightarrow \infty$. ■

Proposition 5 shows that the branching process for budding yeast with proliferative lifespan k , asymptotically grows at the same rate as a binary splitting process with mean number of daughter cells equal to r , in the sense of having the same Malthusian parameter α . However, since the binary splitting population grows as $be^{\alpha t}$ and the budding population as $Cbe^{\alpha t}$ where $C > 1$, the population with the budding process tends to be, on average, larger than the population with the splitting process. Also note that in the binary splitting population, each individual has a positive probability $1 - r/2$ of 0 offspring; hence, this population can go extinct, which is not possible for the budding population. As $k \rightarrow \infty$, $C \rightarrow 1$ and $r \uparrow 2$ so in the limit, budding and binary splitting are equivalent which makes intuitive sense.

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Summary An application of branching processes to a problem in cell biology is described, in which the generalized Fibonacci numbers known as k -nacci numbers play a crucial role. The k -nacci sequence is used to obtain asymptotics, computational formulas, and to justify certain practical simplifications of the biological model. Along the way, an explicit formula for the sum of k -nacci numbers is established.

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