A RECURSION RELATION FOR POPULATIONS OF DIATOMS

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Diatoms are a type of one-celled algae whose unusual reproduction cycle gives rise to an interesting problem in number theory. Sparing the morphological details, the cycle can be described as follows. Each diatom when it reproduces (by cell-division) gives rise to one just like itself, and one a size smaller. This process continues to produce smaller and smaller members of the population until a size is reached where cell-division is no longer physiologically possible. These smallest members then grow until they become as large as the first size, and then begin reproducing normally.

The problem is to determine U_n, the population on the n^{th} generation as a function of both the number of sizes possible, and the growing period.

Let $(m + 1)$ be the number of sizes possible including the growing size, and let r be the number of generations it takes for the smallest size to become mature.

We will show that

$$(1) \qquad U_n(m,r) = 1 + \sum_{j=1}^{m} \sum_{i=0}^{\infty} \binom{n - ir}{im + j} ;$$

and that U_n satisfies the following $m+r)^{th}$ order linear recurrence relation:

$$(2) \qquad \sum_{k=0}^{\infty} (-1)^k \binom{m}{k} U_{(n-k)} = U_{n-(m+r)} \cdot$$

Diagram 1 illustrates the derivation of equation (1). The n^{th} horizontal row represents the population on the n^{th} generation. In the first group of columns, each entry is the sum of the two entries north and northwest of it. This is because for $1 \leq k < m+1$, the k^{th} and $(k-1)^{th}$ sizes each give rise to a k^{th} size, and because in the $(m+1)^{th}$ column we have an individual either growing, or mature; in either case contributing one to the same column in the

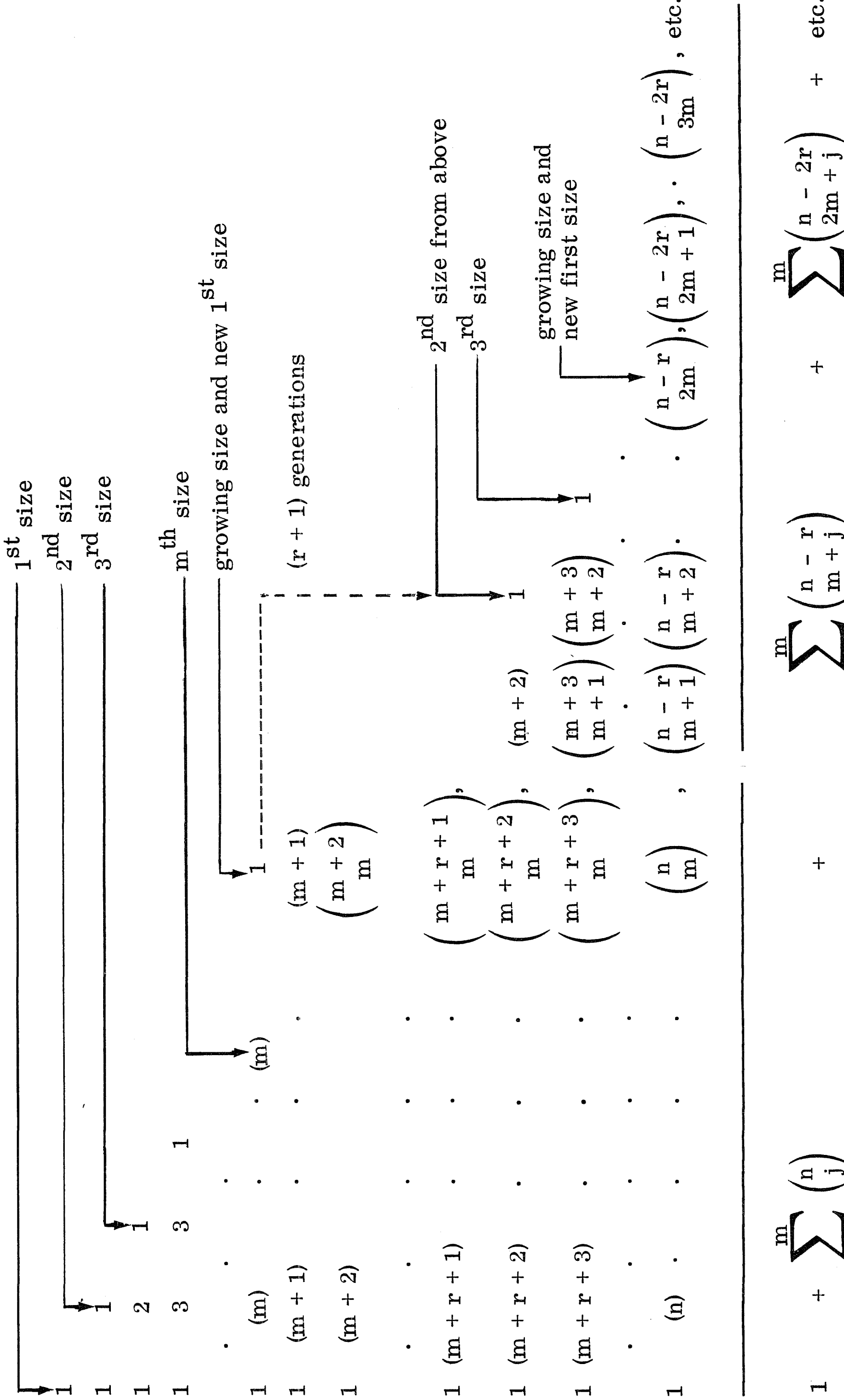
1st size
2nd size
3rd size
mth size
growing size and new 1st size
(r + 1) generations
2nd size from above
3rd size
growing size and new first size
etc.

Diagram 1

next generation. Clearly binomial coefficients are an efficient representation since

$$(3) \qquad \binom{n-1}{k} + \binom{n-1}{k-1} = \binom{n}{k} .$$

In the succeeding groups of columns (only the second group is shown) the same procedure is followed except for the first column of the group. This column represents the second size members which arise from the new first sizes in the last column of the previous group of columns and from the second sizes in the past generation. Thus each element in the first row here is gotten by adding the element north of it to the element $(r + 1)$ places above it and in the last column of the previous group.

Continuing in like manner, we see that in the $(i + 1)^{th}$ group of columns on the n^{th} generation, the top index of the binomial coefficients is $n - ir$, and the bottom index runs from $i(n) + 1$ to $(i + 1)(m)$. This gives equation (1) since all the terms in (1) are zero as soon as the bottom index becomes larger than the top.

We now derive the recurrence relation (2) using the expression in (1) for $U_n(m,r)$. The indices in the double sums on the right will always be from $j = 1$ to m, and $i = 0$ to ∞.

From (1) and (3) we have:

$$(4) \qquad U_n = 1 + \sum_j \sum_i \binom{n - ir}{im + j} = 1 + \sum_j \sum_i \left[\binom{n-1-ir}{im + j} + \binom{n - i - ir}{im + j - 1}\right] ;$$

therefore

$$(5) \qquad U_n - U_{n-1} = \sum_j \sum_i \binom{n - 1 - ir}{im + j - 1} .$$

Now by induction on t we show:

$$(6) \qquad \sum_{k=0}^{\infty} (-1)^k \binom{t}{k} U_{n-k} = \sum_j \sum_i \binom{n - t - ir}{im + j - t} ;$$

$$(7) \qquad = \sum_j \sum_i \left[\binom{n - t - 1 - ir}{im + j - t} + \binom{n - t - 1 - ir}{im + j - t - 1} \right] .$$

Equation (5) shows that (6) holds for $t = 1$, now assume it holds for t; then replacing n with $n - 1$ in (6) and subtracting from (7), we have:

$$\sum_{k=0}^{\infty} (-1)^k \binom{t}{k} U_{n-k} - \sum_{k=0}^{\infty} (-1)^k \binom{t}{k} U_{n-k-1} = \sum_j \sum_i \binom{n - (t+1) - ir}{im + j - (t+1)} .$$

$$\sum_j \sum_i \binom{n - (t+1) - ir}{im + j - (t+1)} = U_n + \sum_{k=1}^{\infty} \left[(-1)^k \binom{t}{k} U_{n-k} + (-1)^k \binom{t}{k-1} U_{n-k} \right]$$

$$= U_n + \sum_{k=1}^{\infty} (-1)^k \binom{t+1}{k} U_{n-k} = \sum_{k=0}^{\infty} (-1)^k \binom{t+1}{k} U_{n-k} ,$$

hence (6) holds for $(t + 1)$ and therefore for all $t \geq 1$.

Now letting $t = m$ in (6), we have:

$$\sum_{k=0}^{\infty} (-1)^k \binom{m}{k} U_{n-k} = \sum_j \sum_i \binom{n - m - ir}{im + j - m}$$

$$= \sum_{j=1}^{m} \sum_{i=0}^{\infty} \binom{n - (m+r) - (i-1)r}{(i-1)m + j}$$

$$= \sum_{j=1}^{m} \binom{n - (m+r) + r}{j - m} + \sum_{j=1}^{m} \sum_{i=1}^{\infty} \binom{n - (m+r) - (i-1)r}{(i-1)m + j}$$

$$= 1 + \sum_{j=1}^{m} \sum_{i=0}^{\infty} \binom{n - (m+r) - ir}{im + j}$$

$$= U_{n-(m+r)} .$$

which establishes (2).

Note that from the diagram we get the following $(m + r)$ initial conditions on $U_n(m,r)$:

$$U_n = \sum_{k=0}^{m} \binom{n}{k} \qquad 1 \le n \le (m + r) ,$$

and also that $U_n(1,1) = F_{n+2}$ where F_n is the n^{th} Fibonacci number. Indeed, the diatom problem is a generalization of the famous Fibonacci rabbit problem.

PART II — GENERATING FUNCTIONS

We may find the generating function for $U_n(m,r)$ by using the recursion above, however it is simpler to calculate the generating functions for each individual size and then add them.

We use the following notation, with m and r fixed.

$a(i,n)$ = total size i in n^{th} generation, $1 \le i \le m$.
$b(j,n)$ = total of growing size which are j generations old in the n^{th} generation, $0 \le j \le r - 1$.

Then we have,

$$\begin{aligned} a(i,n) &= a(i-1,n-1) + a(i,n-1), & a(i,0) &= 0, \quad 2 \le i \le m; \\ a(1,n) &= b(r-1,n-1) + a(1,n-1), & a(1,0) &= 1 . \\ b(j,n) &= b(j-1,n-1) &, \ b(j,0) &= 0, \quad 1 \le j \le r-1; \\ b(0,n) &= a(m,n-1) &, \ b(0,0) &= 0 . \end{aligned} \tag{3}$$

Now we let

$$A(i,x) = \sum_{n=0}^{\infty} a(i,n)x^n \qquad B(j,x) = \sum_{n=0}^{\infty} b(j,n)x^n , \tag{4}$$

which, combined with (3), gives

$$
\begin{aligned}
A(i,x) &= xA(i-1,x) + xA(i,x), \qquad 2 \le i \le m \\
A(1,x) &= xA(1,x) + xB(r-1,x) + 1\,. \\
B(j,x) &= xB(j-1,x) \qquad , \qquad 1 \le j \le r-1 \\
B(0,x) &= xA(m,x)\;.
\end{aligned} \tag{5}
$$

Solving (5), we get

$$
\begin{aligned}
A(m,x) &= \left(\frac{x}{1-x}\right)^{m-1} A(1,x) = \left(\frac{x}{1-x}\right)^{m-1}\left(\frac{x}{1-x}B(r-1,x) + \frac{1}{1-x}\right), \\
&= \left(\frac{x}{1-x}\right)^{m} x^{r-1}B(0,x) + \frac{x^{m-1}}{(1-x)^m} \\
&= \frac{x^{m+r}}{(1-x)^m}A(m,x) + \frac{x^{m-1}}{(1-x)^m}
\end{aligned}
$$

$$
\begin{aligned}
A(m,x) &= \frac{x^{m-1}}{(1-x)^m - x^{m+r}} \\
A(i\,,\,x) &= A(m,x)\left(\frac{1-x}{x}\right)^{m-i} \\
B(j\,,\,x) &= A(m,x)\,x^{j+1}
\end{aligned} \tag{6}
$$

Now we define $P(m,\,r;x)$ as

$$
P(m,r;x) = \sum_{n=0}^{\infty} U_n(m,r)x^n = \sum_{n=0}^{\infty}\left(\sum_{i=1}^{m} a(i,n) + \sum_{j=0}^{r-1} b(j,n)\right)x^n
$$

$$
\begin{aligned}
&= \sum_{i=1}^{m} A(i,x) + \sum_{i=0}^{r-1} B(j,x) \\
&= A(m,x)\left(\sum_{i=1}^{m} \frac{1-x}{x}^{\,m-i} + \sum_{j=1}^{r} x^j\right) \\
&= \frac{(1-x)^m - x^m}{((1-x)^m - x^{m+r})(2x-1)} + \frac{x^m(1-x)^r}{((1-x)^m - x^{m+r})(1-x)}
\end{aligned} \tag{7}
$$

It is of interest to know whether or not the polynomial

$$p(x) = (1 - x)^m - x^{m+r}$$

has any repeated roots. To show that there are none, we set

$$p'(x) = -m(1 - x)^{m-1} - (m + r)x^{m+r-1}$$

and $p(x)$ equal to zero simultaneously, and note that this implies

$$x = \frac{m + r}{r} \quad .$$

This cannot be a root of $p(x)$ since the only possible rational roots of $p(x)$ are ± 1.

Let $\alpha_1, \alpha_2, \cdots, \alpha_{m+r}$ be the roots of $p(x)$ where $|\alpha_i| \leq |\alpha_{i+1}|$. Then

$$P(m, r; x) = g(x) \Bigg/ \prod_{i=1}^{m+r} (x - \alpha_i) \quad ,$$

where $g(x)$ is a polynomial. This expression has the partial fraction expansion,

$$P(m, r; x) = \sum_{i=1}^{m+r} \frac{\beta_i}{(1 - x/\alpha_2)} \quad ,$$

hence

$$P(m, r; x) = \sum_{n=0}^{\infty} \left[\sum_{i=1}^{m+r} \beta_i \left(\frac{1}{\alpha_i} \right)^n \right] x^n \quad ,$$

therefore

$$U_n(m, r) = \sum_{i=1}^{m+r} \beta_i \left(\frac{1}{\alpha_i}\right)^n . \tag{8}$$

From (8) we see that

$$U_n(m, r) = 0\left(\frac{1}{|\alpha_1|^n}\right) .$$

We know that for $r = 0$, $U_n(m,0) = 2^n$ since then we have ordinary cell division. Also, for $r > 0$, $U_n(m,0)$ grows slower than 2^n because of the time lag. Indeed, we now show that for $r > 0$, α_1 is real and $1/2 < \alpha_1 < 1$.

Since

$$(1 - \alpha_i) = \alpha_i^{\frac{m+r}{r}} ,$$

we see that if α_i is real, it must satisfy both $1 - \alpha_i = y$ and

$$\alpha_i^{\frac{m+r}{r}} = y .$$

In Fig. 1 we see that for any m and $r > 0$, there is always a positive real solution, α, to these simultaneous equations where $1/2 < \alpha < 1$. Also, when $m + r$ is even, there is a large (< -1) negative solution. We now show that α is actually the smallest possible in absolute value. We note that for all i,

$$|1 - \alpha_i| = |\alpha_i|^{\frac{m+r}{r}} .$$

Hence $1 - \alpha_i$ must lie on the intersection of the circle about the origin with radius

[Continued on p. 463.]

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