

# Exploring Linear Chain Trickery for Physiologically Structured Populations

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In this paper we address the following question: when can one represent the input-output mapping of an infinite dimensional dynamical system corresponding to a physiologically structured population model by means of a finite dimensional system of ordinary differential equations? We concentrate in particular on sufficient conditions in terms of the individual growth- and death rates.

*Note.* This paper is dedicated to H.A. Lauwerier on the occasion of his 65th birthday and in appreciation of all the methods, techniques and tricks we learned from him.

## 1. PRELUDE: SIMPLIFYING DAPHNIA (ON PAPER)

Suppose we want to model a population of ectothermic invertebrates, e.g. the water flea *Daphnia magna*. Experimentally it appears that reproduction depends on the size of the individual animals and this observation motivated Kooijman & Metz [5] to introduce a size structured model. In Metz & Diekmann [7, I.3] the assumptions underlying the model are described in some detail, so here we restrict ourselves to a mathematical formulation:

$$\begin{cases} \frac{\partial}{\partial t} n(t, l) + \frac{\partial}{\partial l} (v(s, l) n(t, l)) = -\mu(s, l) n(t, l), \\ v(s, l_b) n(t, l_b) = \int_{l_b}^{l_{\max}} \beta(s, l) n(t, l) dl. \end{cases} \quad (1.1)$$

Here  $l$  denotes length and  $s$  substrate (more precisely: concentration of algae). The individual growth, death and reproduction rates are denoted by  $v, \mu$  and  $\beta$ , respectively. The density  $n$  describes the number of *Daphnia* as well as their distribution with respect to length. All individuals are born with length  $l_b$ , and  $l_{\max}$  is the maximal attainable length under abundant food conditions.

To describe some experiments one should consider  $s$  as a given function of



time, but to describe others one has to specify the dynamics of  $s$  as well. In the latter case we take

$$\frac{ds}{dt} = h(s) - \int_{l_b}^{l_{\max}} \gamma(s,l)n(t,l)dl, \quad (1.2)$$

where  $h$  corresponds to the rate of change of the algae concentration in the absence of daphnids and  $\gamma$  is the per capita consumption rate. Under appropriate assumptions on the ingredients  $\nu, \mu, \beta, \gamma$  and  $h$ , (1.1) and (1.2) together generate an infinite dimensional nonlinear dynamical system.

Since daphnids are filter feeders it is reasonable to assume that the consumption rate  $\gamma$  is proportional to the surface area, which in turn is proportional to  $l^2$ . So we put

$$\gamma(s,l) = f(s)l^2. \quad (1.3)$$

If a constant fraction of the ingested energy is allotted to reproduction we may put

$$\beta(s,l) = \alpha f(s)l^2 \quad (1.4)$$

(at this point we deliberately ignore the experimental fact that daphnids don't reproduce if they are still too small; see Metz & Diekmann [7, I.3] for a formulation which does take into account a juvenile period characterized by  $l < l_j$ ). If the rest of the ingested energy is allotted to individual growth and maintenance and if maintenance is proportional to weight, which in turn is proportional to  $l^3$ , we may take

$$\frac{d}{dt}l^3 = 3\delta f(s)l^2 - 3\epsilon l^3$$

and therefore

$$\nu(s,l) = \frac{d}{dt}l = \delta f(s) - \epsilon l. \quad (1.5)$$

Finally we take

$$\mu(s,l) = \mu, \quad \text{a constant.} \quad (1.6)$$

We now introduce

$$N_i(t) = \int_{l_b}^{l_{\max}} l^i n(t,l)dl, \quad i = 0, 1, 2 \quad (1.7)$$

and find, using (1.1)-(1.7) and some straightforward integrations (by parts), that  $(N,s)$  satisfies the *closed* system of ordinary differential equations



$$\begin{aligned}
\frac{dN_0}{dt} &= \alpha f(s)N_2 - \mu N_0 \\
\frac{dN_1}{dt} &= l_b \alpha f(s)N_2 - \delta f(s)N_0 - (\mu + \epsilon)N_1 \\
\frac{dN_2}{dt} &= l_b^2 \alpha f(s)N_2 + 2\delta f(s)N_1 - (\mu + 2\epsilon)N_2 \\
\frac{ds}{dt} &= h(s) - f(s)N_2.
\end{aligned} \tag{1.8}$$

The powerful qualitative theory of finite dimensional dynamical systems can now be used to study (1.8) and likewise one can choose from a multitude of well established schemes to study (1.8) numerically (De Roos [9] exploits this fact to investigate the accuracy of the escalator boxcar train, a method to solve the partial differential equation (1.1) numerically).

Of course, neglecting the juvenile period has consequences, the main difference between the present model and the full one being that the latter not only allows the occurrence of predator prey oscillations due to the lag in recovery of the food population, but in addition oscillations related to the development lag (see Metz, De Roos & Van den Bosch [8] or De Roos, Diekmann & Metz [10]).

## 2. INTRODUCTION: GENERAL MODELS AND TRACTABLE SPECIAL CASES

Every painter needs technical tools to materialize the views he has in mind. Likewise, to practise the art of modelling natural phenomena one needs methods, techniques and tricks. This paper is about a coherent collection of tricks which reduce certain infinite dimensional dynamical systems to finite dimensional ones. In particular, the paper concentrates on the applicability of such tricks in the context of physiologically structured population models (Metz & Diekmann [7]).

Before embarking upon the mathematical aspects, we want to make some remarks about modelling in general in order to bring the underlying ideas in perspective. First of all, the structured population methodology provides a framework for strategic modelling. By this we mean the building of master models which, except in those parts representing the specific mechanistic feature about which we wish to obtain information and understanding, are as general as possible. Within such a framework we can try to prove general theorems and develop general concepts.

If we are lucky, the specific mechanism under investigation, by its very nature, allows some sort of model reduction (an example is provided by the use of an equivalent ‘age’ ( $:=$  time elapsed since infection) representation in the Kermack-McKendrick epidemic model, Metz & Diekmann [7, IV.4.1]) and completely general assertions can rigorously be shown to be valid. Usually, however, it is very difficult, if not impossible, to obtain such strong results. In that case we may start considering simplifications chosen for their mathematical convenience (these we may call tactic models with a strategic objective as



opposed to tactic models with a concrete objective, viz. prediction and/or testing). Here our hope is set on robustness: we expect that the results derived in the context of the simplified models are more or less typical for (some subclass of) the full master model. This hope seems especially justified when the results allow a mechanistic interpretation (an example is provided by the various criteria specifying the qualitative properties of the bifurcation diagram for the cannibalism model of Van den Bosch, De Roos & Gabriel [1]).

As a warning note we recall from Section 1 that De Roos, Diekmann & Metz [10], report a certain type of oscillations for the *Daphnia* model with a juvenile period taken into account for which there is no counterpart in the special case described by (1.8).

Linear chain trickery provides one particular means for carrying out mathematical simplifications. The name arose in the context of delay equations, see MacDonald [6].

### 3. AN ABSTRACT FORMULATION OF PHYSIOLOGICALLY STRUCTURED POPULATION MODELS

Let the individuals of a population be characterized by finitely many variables, which together we call the *i*-state. So the set of feasible *i*-states  $\Omega$  is a nice subset of  $\mathbb{R}^n$ , for some  $n$ . At the individual level a model amounts to a specification of (i) the rate of *i*-state change, (ii) the deathrate, (iii) the birthrate and in particular how (i), (ii) and (iii) depend on the *i*-state and the prevailing environmental conditions. The latter are described by a, possibly even infinite dimensional, variable  $E$ . In the case of the birthrate we have to specify the (distribution of the) state at birth as well.

Once we have a model at the individual level we can immediately derive balance laws doing the necessary bookkeeping. These balance laws generate the time evolution at the population level. There are two types of balance laws, related to each other by duality. The Kolmogorov backward equation is concerned with the clan mean of a continuous function on  $\Omega$ . The Kolmogorov forward equation describes infinitesimal changes in the measure which assigns to every measurable subset of  $\Omega$  the number of individuals which have at that instant an *i*-state which belongs to the particular subset. This measure is called the *p*-state (*p* for population) and the space  $M(\Omega)$  of regular Borel measures on  $\Omega$  is called the *p*-state space. Frequently (but not always) we can restrict our attention to densities and formulate the Kolmogorov forward equation for  $L_1(\Omega)$ .

We can use duality since for  $E$  a given function of time, by assumption, the equations are linear. Some environmental variables, like food, are in turn influenced by the population, e.g. through consumption. Thus nonlinear problems come into being by allowing feedbacks through the environment.

Formally at least, the Kolmogorov forward equation can be written as

$$\frac{dn}{dt} = A(E)^* n. \quad (3.1)$$

Quite in general we have a decomposition



$$A(E) = A_0(E) + B(E) \quad (3.2)$$

where  $A_0$  describes  $i$ -state changes and deaths and  $B$  represents births (the importance of this decomposition derives from the fact that for  $B = 0$  we can write down explicit solutions by integration along characteristics, i.e. following cohorts). The mathematical theory to provide a rigorous justification and interpretation is still in its infancy. First steps towards a general framework have been made in Clément et al. [2] (see Diekmann [3] for a survey), but much work remains to be done. In the present paper we simply ignore all problems related to existence and uniqueness of solutions and to the precise interpretation of the abstract differential equation. We shall restrict ourselves to formal manipulations.

#### 4. AN ABSTRACT FORMULATION OF LINEAR CHAIN TRICKERY

Let  $P: M(\Omega) \rightarrow \mathbb{R}^k$  be a mapping such that

$$PA(E)^* = M(E)P \quad (4.1)$$

for some family  $M(E)$  of  $k \times k$  matrices. Define

$$N(t) = Pn(t), \quad (4.2)$$

then (3.1) implies that  $N$  satisfies the ODE

$$\frac{dN}{dt} = M(E)N. \quad (4.3)$$

REMARK. If we assume that

$$Px^* = \langle \Phi, x^* \rangle \quad (4.4)$$

for some  $k$ -vector  $\Phi$  with components  $\phi_i \in X$  (note that this is an assumption since  $X$  need not be reflexive), then we can reformulate (4.1) as

$$A(E)\Phi = M(E)\Phi, \quad (4.5)$$

provided  $\Phi \in D(A(E))$  for all  $E$ . Actually  $\bigcap_E D(A(E))$  may be empty. However, within the context of dual semigroups one can extend  $A(E)$  to an operator  $A(E)^{\odot*}$  which has its range in a larger space  $X^{\odot*}$  and therefore has larger domain as well (see Clément et al. [2] or Diekmann [3]). One can then replace (4.5) by

$$A(E)^{\odot*}\Phi = M(E)\Phi. \quad (4.6)$$

In the following we shall restrict our attention to mappings  $P$  of the form (4.4) and we shall not go into the distinction between (4.5) and (4.6) (in fact we shall omit the precise definition of domains of unbounded operators).

Next assume that  $E$  is finite dimensional and that feedback through the environment is incorporated by allowing the equations for  $E$  to depend on  $C(E)^*n$ , where  $C(E)^*$  maps  $M(\Omega)$  into  $\mathbb{R}^m$  for some  $m$  (one may call  $C(E)^*$  the output mapping). If a family  $\Gamma(E)$  of  $k \times m$  matrices exists such that



$$C(E)^* = \Gamma(E)P \quad (4.7)$$

then  $C(E)^*n = \Gamma(E)Pn = \Gamma(E)N$  and consequently a coupled *finite dimensional* system for  $N$  and  $E$  describes the interaction completely. Once  $E$  is determined by solving this reduced system, we can consider

$$\frac{dn}{dt} = A(E)^*n \quad (4.8)$$

as a non-autonomous (i.e. time-dependent) but *linear* equation. A special case of particular importance arises if one can conclude from the  $(N, E)$ -system that  $E$  approaches a limit (or a periodic solution) as  $t \rightarrow \infty$ . In that case the linear equation for  $n$  is asymptotically autonomous (periodic) and one can base further conclusions on the known asymptotic behaviour for these special situations.

EXAMPLE 1. Consider a cell population with size structure and assume that a mother cell divides into two exactly equal daughter cells. Then the forward equation for densities reads

$$\frac{\partial n}{\partial t}(t, x) = -\frac{\partial}{\partial x}(g(x, E)n(t, x)) - \beta(x, E)n(t, x) + 4\beta(2x, E)n(t, 2x) \quad (4.9)$$

(see Heijmans [4], Metz & Diekmann [7, I.4, VI.5] and the references given there). Introducing the total biomass operator

$$P\psi = \int_{\frac{1}{2}x_{\min}}^{x_{\max}} x\psi(x)dx \quad (4.10)$$

we note that

$$P(-\beta(\cdot, E)\psi(\cdot) + 4\beta(2\cdot, E)\psi(2\cdot)) = 0$$

since mass is conserved in the division process. In other words,  $PB(E)^* = 0$ . Assuming

$$g(x, E) = h(E)x$$

we get

$$\begin{aligned} PA_0(E)^*\psi &= -\int_{\frac{1}{2}x_{\min}}^{x_{\max}} x \frac{\partial}{\partial x}(h(E)x\psi(x))dx \\ &= h(E) \int_{\frac{1}{2}x_{\min}}^{x_{\max}} x\psi(x)dx = h(E)P\psi \end{aligned}$$

(provided  $\psi(\frac{1}{2}x_{\min}) = \psi(x_{\max}) = 0$ ). Combining these two observations we have

$$PA(E)^* = h(E)P.$$



Next interpret  $E$  as the concentration of the limiting substrate (so  $E$  is one-dimensional) and assume that the individual growthrate is proportional to the individual nutrient uptake rate. Then

$$C(E)^*n = kh(E)Pn$$

with  $k$  a conversion factor. Finally, assume chemostat dynamics. Then

$$\begin{aligned}\frac{dN}{dt} &= h(E)N - DN, \\ \frac{dE}{dt} &= D(E^i - E) - kh(E)N,\end{aligned}$$

where  $D$  is the dilution rate and  $E^i$  is the concentration of the limiting substrate in the inflowing fluid (note that we have now added a term  $-Dn(t, x)$  to the right hand side of (4.9)). Under appropriate assumptions on  $h$ , the ODE system has a globally stable steady state.  $\square$

Under further conditions one can obtain stronger results. The idea is that one can write down the zero'th generation, i.e. the solution of  $dn_0/dt = A_0(E)^*n_0$ , explicitly and that  $n_0$  tends to zero as  $t \rightarrow \infty$  (recall that  $A_0$  incorporates only  $i$ -state change and death, no birth; in fact the weaker condition that  $B(E)^*n_0(t) \rightarrow 0$  as  $t \rightarrow \infty$  is sufficient for our purposes). So whenever  $B(E)^* = \Lambda(E)P$  for some family of mappings  $\Lambda(E): \mathbb{R}^k \rightarrow M(\Omega)$  one can write down the solution  $n(t)$  explicitly in the form of a variation-of-constants formula involving  $n_0(t)$  and  $N(t)$ . Motivated by this observation we first look for  $P: M(\Omega) \rightarrow \mathbb{R}^k$  and  $k \times k$  matrices  $H(E)$  such that

$$PA_0(E)^* = H(E)P. \quad (4.11)$$

If then, moreover,  $B(E)^* = \Lambda(E)P$  and  $C(E)^* = \Gamma(E)P$  the infinite dimensional dynamical system is reduced to a finite dimensional one and, conversely, one can recover the solution of the original system completely from the solution of the ODE system by using the (explicit) variation-of-constants formula for the growth-death part  $A_0(E)^*$ .

## 5. SUFFICIENT CONDITIONS FOR LINEAR CHAIN TRICKERY

Assume that the  $i$ -state space is one-dimensional. Then

$$(A_0(E)\phi)(x) = v(x, E)\phi'(x) - \mu(x, E)\phi(x) \quad (5.1)$$

where  $v$  is the individual growthrate and  $\mu$  the per capita deathrate.

We first restrict ourselves to the case where  $P$  has one-dimensional range. The question then is: under which conditions on  $v$  and  $\mu$  can we find a (continuous) function  $\phi(x)$  and a function  $\lambda(E)$  such that

$$v(x, E)\phi'(x) - \mu(x, E)\phi(x) = \lambda(E)\phi(x) \quad ? \quad (5.2)$$

If we rewrite (5.2) in the form

$$\frac{\mu(x, E) + \lambda(E)}{v(x, E)} = \frac{\phi'(x)}{\phi(x)} \quad (5.3)$$



we see that a necessary as well as sufficient condition is that for some function  $\lambda(E)$  the function  $\frac{\mu(x,E)+\lambda(E)}{v(x,E)}$  is independent of  $E$  (indeed, if we baptize this function  $f(x)$  we can choose  $\phi(x) = \exp \int^x f(\xi) d\xi$ .)

EXAMPLE 2. Age-dependent population dynamics.

If  $v(x,E) = 1$  the condition is simply that  $\mu$  is the sum of a function of  $x$  (in this context we prefer to call  $x$   $a$ ) and a function of  $E$ . Note that  $\lambda$  is determined modulo additive constants only and that, as a consequence, we have a one-parameter family of  $\phi$ 's. This gives greater flexibility for satisfying the remaining conditions for  $B(E)^*$  and  $C(E)^*$ .  $\square$

EXAMPLE 3. Size-dependent population dynamics.

If, for instance,  $\mu$  is independent of  $x$  we can choose  $\lambda(E) = -\mu(E)$  and  $f(x) = 0$ , hence  $\phi(x) = 1$ , which simply means that  $N$  is total population. The conditions on  $B$  and  $C$  then require that the per capita contribution to the birthrate as well as the per capita consumption rate are independent of  $x$ .  $\square$

As a second special case we don't restrict the dimension of the range of  $P$  but concentrate on age  $a$  as the  $i$ -state. Then

$$\Phi'(a) - \mu(a,E)\Phi(a) = H(E)\Phi(a). \quad (5.4)$$

Let us first take some arbitrary but fixed  $E_0$  then

$$\Phi(a) = e^{\int_0^a \mu(\alpha, E_0) d\alpha} e^{H(E_0)a} \Phi(0). \quad (5.5)$$

Substituting this expression into (5.4) we find

$$(\mu(a, E_0) - \mu(a, E))\Phi(a) = (H(E) - H(E_0))\Phi(a) \quad (5.6)$$

or, in other words,  $\Phi(a)$  is an eigenvector of  $H(E) - H(E_0)$  with corresponding eigenvalue  $\mu(a, E_0) - \mu(a, E)$ . For fixed  $E_0$  and  $E$  the eigenvalues form a discrete set. On the other hand it is reasonable to assume that  $a \mapsto \mu(a, E_0) - \mu(a, E)$  is continuous. But a continuous function taking values in a discrete set is constant. So necessarily

$$\mu(a, E) = \mu(a, E_0) + \lambda(E), \quad \text{with } \lambda(E_0) = 0. \quad (5.7)$$

Then we can simply take

$$H(E) = H(E_0) - \lambda(E)I \quad (5.8)$$

and verify that (5.5) implies (5.4) when (5.7) and (5.8) hold. We conclude that in the age-dependent case (5.7) is a necessary and sufficient condition for this part of the linear chain trickery and that we still have a vector  $\Phi(0)$  and a matrix  $H(E_0)$  at our disposal to satisfy the further conditions imposed by the birth and output operators.

If we try to do the same thing for general one-dimensional  $i$ -state  $x$ , the



analogue of (5.6) is

$$\left[ \frac{v(x,E)}{v(x,E_0)} \mu(x,E_0) - \mu(x,E) \right] \Phi(x) = (H(E) - \frac{v(x,E)}{v(x,E_0)} H(E_0)) \Phi(x), \quad (5.9)$$

and our argument breaks down since the matrix at the right hand side is, in general, not independent of  $x$  (it is only in the case of physiological age, i.e.  $v(x,E) = a(E)f(x)$ ). The following example shows that this indeed makes an essential difference.

**EXAMPLE 4.** Once more, size-dependent population dynamics.

We still assume that  $\mu$  is independent of  $x$ . We choose  $k = 2$  and  $\phi_1(x) = 1$ ,  $\phi_2(x) = x$ . We want that, for some  $2 \times 2$  matrix  $H(E)$

$$v(x,E) \begin{bmatrix} 0 \\ 1 \end{bmatrix} - \mu(E) \begin{bmatrix} 1 \\ x \end{bmatrix} = H(E) \begin{bmatrix} 1 \\ x \end{bmatrix} = \begin{bmatrix} h_{11}(E) + h_{12}(E)x \\ h_{21}(E) + h_{22}(E)x \end{bmatrix}. \quad (5.10)$$

Choosing  $h_{12}(E) = 0$  and  $h_{11}(E) = \mu(E)$  we have an identity for the first component without any requirement for  $v$ . However, the second component requires that  $v$  is of the form

$$v(x,E) = a(E) + b(E)x. \quad (5.11)$$

We then choose  $h_{21}(E) = a(E)$  and  $h_{22}(E) = b(E) - \mu(E)$ . So

$$H(E) = \begin{bmatrix} 0 & 0 \\ a(E) & b(E) \end{bmatrix} - \mu(E)I,$$

which is not of the form (5.8).  $\square$

Note that we can immediately extend the example to any number of dimensions by choosing

$$\Phi(x) = (1, x, \frac{1}{2}x^2, \dots)^T.$$

Moreover, one can employ an  $E$  independent change of  $i$ -state variable to bring a growthrate  $v$  in the form (5.11). For example, the growth laws most commonly encountered in the literature

- (i) von Bertalanffy:  $\frac{dy}{dt} = \alpha y^{2/3} - \beta y$ ,
- (ii) logistic:  $\frac{dy}{dt} = \alpha y - \beta y^2$ ,
- (iii) Gompertz:  $\frac{dy}{dt} = \alpha y - \beta y \log y$ ,

can all be linearized:

- (i)  $x = y^{1/3} \Rightarrow \frac{dx}{dt} = \frac{1}{3}(\alpha - \beta x)$ ,
- (ii)  $x = \frac{1}{y} \Rightarrow \frac{dx}{dt} = \beta - \alpha x$ ,



$$(iii) \quad x = \log y \Rightarrow \frac{dx}{dt} = \alpha - \beta x,$$

(we thank Y. Iwasa for bringing (ii) and (iii) to our attention).

Modulo such changes of  $i$ -state variable, Example 4 is the only example we know in which a nontrivial higher dimensional  $\Phi$  occurs. So far our attempts to formulate and demonstrate *necessary* conditions (perhaps under some *a priori* restrictions), which would imply that there are no other examples, have not been successful.

In conclusion of this section we present one example with a higher dimensional  $i$ -state space. The analogue of (5.1) is

$$(A_0(E)\phi)(x) = v(x, E) \cdot \nabla \phi(x) - \mu(x, E)\phi(x) \quad (5.12)$$

or, in words:  $v\phi'$  is replaced by the directional derivative in the direction of the vector field  $v$ .

EXAMPLE 5. Consider two-dimensional  $x$  and let  $v$  be given by

$$v(x, E) = \begin{bmatrix} a(E) + b(E)x_1 \\ c(E) \end{bmatrix}.$$

Define

$$\Phi(x) = (1, x_1, x_1^2, e^{-kx_2}, x_1 e^{-kx_2}, x_1^2 e^{-kx_2})^T,$$

and

$$H(E) = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 \\ a & b & 0 & 0 & 0 & 0 \\ 0 & 2a & 2b & 0 & 0 & 0 \\ 0 & 0 & 0 & -kc & 0 & 0 \\ 0 & 0 & 0 & a & (b - kc) & 0 \\ 0 & 0 & 0 & 0 & 2a & 2b - kc \end{bmatrix}.$$

A straightforward calculation then shows that

$$v(x, E) \cdot \nabla \Phi(x) = H(E)\Phi(x)$$

which is the required relation for  $\mu = 0$ . When  $\mu$  is non-zero but still independent of  $x$  we can redefine  $H(E)$  by subtracting  $-\mu(E)I$ .

The biological interest of this example is that we may interpret  $x_1$  as size and  $x_2$  as physiological age. Moreover  $\Phi$  is chosen in such a way that we can choose

$$\beta(x, E) = f(E)(1 - e^{-kx_2})x_1^2$$

as an age and size dependent birthrate of individuals.



## 6. DISCUSSION

Understanding the precise nature of necessary and sufficient conditions for linear chain trickery may be important for two reasons. First of all it should yield a *complete* catalogue of cases in which a reduction to finite dimensions is possible. No doubt this catalogue will contain useful cases which thus far escaped our attention (like the case from Example 5). Secondly it will show which (classical) ODE models can be reinterpreted as reduced structured models. (In our, admittedly somewhat biased, opinion the justification of any ODE model should derive from the fact that such an interpretation is possible.)

In this paper we have made a first step towards the derivation of necessary and sufficient conditions, but we are still far from reaching our final goal. However, we plan to keep on working at it.

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