Appendix: Ribosome Flow Model with Extended Objects

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A. Proofs

Proof of Prop. 1. Combining (4) and (6) yields

\[
\dot{y}_i = \sum_{m=1}^{i} \dot{x}_m = \lambda_0 (1 - y_\ell) - \lambda_i x_i (1 - y_{i+\ell}), \quad 1 \leq i \leq \ell,
\]

\[
\dot{y}_i = \sum_{m=1-\ell+1}^{i} \dot{x}_m = \lambda_{i-\ell} x_{i-\ell} (1 - y_i) - \lambda_i x_i (1 - y_{i+\ell}), \quad \ell < i \leq n. \tag{A.1}
\]

By the definition of \( y_i \), \( x_i = y_i - y_{i-1} + x_{i-\ell} \), and iterating this yields

\[
x_i = \sum_{k=0}^{[i-\ell/\ell]} (y_{i-k\ell} - y_{i-k\ell-1}). \tag{A.2}
\]

Substituting this in (A.1) yields (11).

Proof of Prop. 2. Consider the RFMEO with \( x(0) \in \partial H \). Then \( y(0) = P x(0) \), and there exists an index \( i \) such that either \( x_i(0) \in \{0, 1\} \) or \( y_i(0) \in \{0, 1\} \) and all the other entries of \( x(0) \) and \( y(0) \) are between zero and one. The proof is based on computing the derivatives of the state-variables at time zero, and showing that state-variables that are zero [one] become strictly larger than zero [strictly smaller than one] at time \( 0^+ \). We assume throughout that \( \ell \geq 2 \), as otherwise the RFMEO reduces to the RFM and then the proof follows from the results in [4]. We consider several cases.

Case 1. Suppose that \( y_\ell(0) = 0 \). This implies in particular that \( x_\ell(0) = 0 \). By (A.1),

\[
\dot{y}_\ell(0) = \lambda_0 (1 - y_\ell(0)) - \lambda_\ell x_\ell(0)(1 - y_{2\ell}(0)) = \lambda_0.
\]

Thus, \( y_\ell(0^+) > 0 \). Note that this calculation also implies that for any \( \tau > 0 \) there exists \( \varepsilon_\ell = \varepsilon_\ell(\tau) > 0 \) such that \( y_\ell(t, a) \geq \varepsilon_\ell \) for all \( t \geq \tau \) and all \( a \in H \).

Case 2. Suppose that \( y_{\ell+1}(0) = 0 \). This implies in particular that \( x_{\ell+1}(0) = 0 \), so \( y_\ell(0) = y_\ell(0) - y_{\ell+1}(0) = x_1(0) - x_{\ell+1}(0) = x_1(0) \). By (A.1),

\[
\dot{y}_{\ell+1}(0) = \lambda_1 x_1(0)(1 - y_{\ell+1}(0)) - \lambda_{\ell+1} x_{\ell+1}(0)(1 - y_{2\ell+1}(0)) = \lambda_1 y_\ell(0).
\]
Combining this with the result in Case 1 implies that for any $\tau > 0$ there exists $\varepsilon_{\ell+1} = \varepsilon_{\ell+1}(\tau) > 0$ such that $y_{\ell+1}(t, a) \geq \varepsilon_{\ell+1}$ for all $t \geq \tau$ and all $a \in H$.

Continuing in this fashion shows that for any $\tau > 0$ there exists $\varepsilon = \varepsilon(\tau) > 0$ such that $y_i(t, a) \geq \varepsilon$ for all $i \in \{\ell, \ell + 1, \ldots, n\}$, all $t \geq \tau$, and all $a \in H$.

Case 3. Suppose that $x_j(0) = 0$ for some $j$. Then there exists a minimal index $i$ such that $x_i(0) = 0$. If $i = n$ then (6) yields

$$\dot{x}_n(0) = \lambda_{n-1}x_{n-1}(0) - \lambda_n x_n(0)$$

By the definition of $i$, $x_n(0) > 0$ and thus $x_n(0^+) > 0$.

Now suppose that $i = n - 1$. Then (6) yields

$$\dot{x}_{n-1}(0) = \lambda_{n-2}x_{n-2}(0)(1 - y_{n+\ell-2}(0)) - \lambda_{n-1}x_{n-1}(0)$$

$$= \lambda_{n-2}x_{n-2}(0)(1 - y_{n+\ell-2}(0)).$$

By the definition of $i$, $x_{n-2}(0) > 0$. If $\ell > 2$ then $1 - y_{n+\ell-2}(0) = 1$, and thus $x_{n-1}(0^+) > 0$. If $\ell \leq 2$ then $1 - y_{n+\ell-2}(0) = 1 - y_n(0) = 1 - x_n(0) - x_{n-1}(0) = 1 - x_n(0)$. Thus, if $x_n(0) < 1$ then $x_{n-1}(0^+) > 0$.

Consider the case $x_n(0) = 1$. Then $y_n(0) = x_{n-1}(0) + x_n(0) = 1$, so

$$\dot{y}_n(0) = \lambda_{n-\ell}x_{n-\ell}(0)(1 - y_n(0)) - \lambda_{n}x_n(0)$$

$$= -\lambda_{n}.$$ 

This means that $y_n(0^+) < 1$, so again we conclude that $x_{n-1}(0^+) > 0$.

Continuing in this fashion shows that if $x_j(0) = 0$ for some $j$ then $x_j(0^+) > 0$. The analysis in all the other relevant cases is very similar, and thus omitted.

**Proof of Prop. 3.** This follows from the fact that $H$ is compact, convex and with a repelling boundary; see [6, Thm. 2] (see also [5]).

**Proof of Prop. 4.** Pick $\varepsilon, \tau > 0$ and $a, b \in H$. By Prop. 3, there exists $\delta = \delta(\tau) \in (0, 1/2)$ such that for all $i$ and all $t \geq \tau$,

$$\delta \leq x_i(t), y_i(t) \leq 1 - \delta.$$  \hspace{1cm} (A.3)

Write the $q_j$s in (6) as

$$q_j(x) = \lambda_j x_j(1 - y_{j+\ell})$$

$$= \eta_j x_j(1 - x_{j+1}),$$

where $\eta_j(t) := \lambda_j \frac{1 - y_{j+\ell}(t)}{1 - x_{j+1}(1)}$. Note that (A.3) implies that

$$0 < \lambda_j \frac{\delta}{1 - \delta} \leq \eta_j(t) \leq \lambda_j \frac{1 - \delta}{\delta} < \infty$$  \hspace{1cm} (A.4)

for all $j$ and all $t \geq \tau$. Using this notation, the RFMEO in (6) can be written as the time-varying system

$$\dot{x}_i = \eta_{i-1}x_{i-1}(1 - x_i) - \eta_j x_j(1 - x_{j+1}).$$

This means that for all $t \geq \tau$ the RFMEO can be interpreted as an RFM with time-varying transition rates $\eta_j(t)$ that, by (A.4), are uniformly bounded and uniformly separated from zero for all $t \geq \tau$. Now the results in [4] imply that there exists $\gamma := \gamma(\varepsilon)$ such that after time $\tau$ the solutions are contractive with overshoot $(1 + \varepsilon)$, and this completes the proof.

**Proof of Prop. 5.** Consider two RFMEOs, both with the same dimension $n$ and particle size $\ell$. The first with rates $\lambda_0, \ldots, \lambda_n$, admits a steady-state density $\bar{e}$, and a steady-state production rate $\bar{R}$, and the second with rates $\tilde{\lambda}_0, \ldots, \tilde{\lambda}_n$, admits a steady-state density $\tilde{e}$ and a steady-state production rate $\tilde{R}$. Assume that
there exists an index \( j \in \{0, \ldots, n\} \), such that \( \tilde{\lambda}_i = \lambda_i \) for all \( i \neq j \), and

\[
\tilde{\lambda}_j > \lambda_j. \tag{A.5}
\]

We need to show that \( \tilde{R} > R \). Seeking a contradiction, assume that

\[
\tilde{R} \leq R. \tag{A.6}
\]

We start with the case \( j = n \). Combining (A.6), (A.5) and (19) implies that \( \tilde{e}_n < e_n \), and \( \tilde{e}_{n-k} \leq e_{n-k} \), \( k = 1, \ldots, \ell - 1 \). This means that \( \tilde{y}_n < y_n \), and combining this with (A.6) and (19) implies that \( \tilde{e}_{n-\ell} < e_{n-\ell} \), and so \( \tilde{y}_{n-1} < y_{n-1} \). Continuing in this way yields \( \tilde{e}_j < e_j \), \( j = 1, \ldots, n - \ell \). In particular, \( \tilde{e}_1 + \cdots + \tilde{e}_\ell < e_1 + \cdots + e_\ell \), and using (19) results in \( \tilde{R} > R \). This contradicts (A.6), and so we conclude that \( \tilde{R} > R \) in the case where \( \tilde{\lambda}_n > \lambda_n \).

Using the same approach for any \( j \in \{0, \ldots, n\} \), while combining the assumption in (A.6) with (A.5) and (19), yields

\[
\tilde{y}_k \leq y_k, \quad k = j + \ell, \ldots, n, \\
\tilde{y}_k < y_k, \quad k = \ell, \ldots, j + \ell - 1. \tag{A.7}
\]

If \( j > 0 \) then using \( k = \ell \) in (A.7) yields \( \tilde{e}_1 + \cdots + \tilde{e}_\ell < e_1 + \cdots + e_\ell \), thus \( \tilde{R} > R \), contradicting (A.6). If \( j = 0 \) then using \( k = \ell \) in (A.7) yields \( \tilde{e}_1 + \cdots + \tilde{e}_\ell \leq e_1 + \cdots + e_\ell \), but since \( \lambda_0 > \lambda_0 \), this again yields \( \tilde{R} > R \), contradicting (A.6). We conclude that \( \tilde{R} > R \).

Proof of Prop. 6. Consider (19) with \( \lambda_0 = \cdots = \lambda_n \). Then

\[
e_{n-\ell+1} = \cdots = e_n. \tag{A.8}
\]

Since \( e_{n-\ell}(1 - e_{n-\ell+1} - \cdots - e_n) = e_{n-\ell}(1 - z_n) = e_{n-\ell+1} \), and \( z_n \in (0, 1) \), it follows that

\[
e_{n-\ell} > e_{n-\ell+1}. \tag{A.9}
\]

and combining this with (A.8) implies that

\[
z_{n-1} > z_n. \tag{A.10}
\]

Now, since \( e_{n-\ell-1}(1 - e_{n-\ell} - \cdots - e_{n-1}) = e_{n-\ell-1}(1 - z_{n-1}) = e_{n-\ell}(1 - z_n) \), using (A.10) and the fact that \( z_{n-1}, z_n \in (0, 1) \) imply that \( e_{n-\ell-1} > e_{n-\ell} \) and thus \( z_{n-2} > z_{n-1} \). Continuing in this way completes the proof.

Proof of Prop. 7. Let \( [\tilde{e}] \) denote the steady-state reader density in the RFMEO [RFM]. We need to show that \( \tilde{R} > R \). Seeking a contradiction, assume that

\[
\tilde{R} \leq R. \tag{A.11}
\]

Combining this with (19) for both the RFMEO with particle size \( \ell \) and with particle size one (i.e. the RFM), it follows that \( \lambda_0(1 - \tilde{e}_1) \leq \lambda_0(1 - e_1 - \cdots - e_\ell) \), thus

\[
\tilde{e}_1 \geq e_1 + \cdots + e_\ell,
\]

and since \( e \in \text{Int}(H) \) this yields

\[
\tilde{e}_1 > e_1. \tag{A.12}
\]

Using (19), (A.11), and (A.12), it follows that

\[
\tilde{e}_2 > e_2 + \cdots + e_{\ell+1},
\]

and since \( e \in \text{Int}(H) \) this yields

\[
\tilde{e}_2 > e_2.
\]
Continuing in this way yields
\[ e_j > e_j + \cdots + e_{j+\ell-1}, \quad j = 2, \ldots, n - \ell + 1, \]
so in particular,
\[ e_{n-\ell+1} > e_{n-\ell+1} + \cdots + e_n. \]

On the other-hand using (A.11) and comparing the last \( \ell \) equations in (19) for both the RFMEO with particle size \( \ell \) and with particle size one (i.e. the RFM), yields
\[
\begin{align*}
\bar{e}_{n-\ell+1}(1 - \bar{e}_{n-\ell+2}) & \leq e_{n-\ell+1}, \\
\bar{e}_{n-\ell+2}(1 - \bar{e}_{n-\ell+3}) & \leq e_{n-\ell+2}, \\
& \vdots \\
\bar{e}_{n-1}(1 - \bar{e}_n) & \leq e_{n-1}, \\
\bar{e}_n & \leq e_n.
\end{align*}
\]

Now combining (A.15) with (A.14) yields
\[
\bar{e}_{n-\ell+2}(1 - \bar{e}_{n-\ell+1}) + \bar{e}_{n-\ell+3}(1 - \bar{e}_{n-\ell+2}) + \cdots + \bar{e}_n(1 - \bar{e}_{n-1}) < 0. \tag{A.16}
\]

However, since \( \bar{e} \in \text{Int}(H) \), the term on the left-hand side here must be strictly positive. This contradiction completes the proof.

\section*{B. RFMEO as a Mean-Field Approximation of TASEPEO}

In this appendix, we show how the RFMEO can be derived from TASEPEO. We use a notation that is standard in the TASEPEO literature.

Consider TASEPEO with \( N \) sites, rates \( \mu \) defined in (1), extended object size \( \ell \), and under the assumption that the reader is located at the left-most site of the object. Following MacDonald et. al. [2] (see also [3]) the current from site \( i \) to site \( i + 1 \) at time \( t \) is given by (for simplicity we ignore boundary cases):
\[
J_{i\rightarrow i+1}(t) = \gamma_i \Pr(\text{site } i \text{ has a reader and site } i + \ell \text{ is empty}) \\
= \gamma_i \Pr(\text{site } i \text{ has a reader}) \Pr(\text{site } i + \ell \text{ is empty } | \text{ site } i \text{ has a reader}),
\]
\tag{A.17}
where \( \Pr(a) [\Pr(a|b)] \) denotes the probability of event \( a \) [the conditional probability of event \( a \) given event \( b \)] at time \( t \). Since the conditional probability in (A.17) is difficult to estimate, we apply what [1] calls a naive mean-field approximation, and replace (A.17) by:
\[
J_{i\rightarrow i+1}(t) = \gamma_i \Pr(\text{site } i \text{ has a reader}) \Pr(\text{site } i + \ell \text{ is empty}) \\
= \gamma_i \Pr(\text{site } i \text{ has a reader}) \left( 1 - \sum_{k=0}^{\ell-1} \Pr(\text{site } i + \ell - k \text{ has a reader}) \right).
\]
\tag{A.18}
We approximate the probabilities above by averaging the binary reader occupancies over an ensemble of TASEPEO systems, i.e. we replace \( \Pr(\text{site } i \text{ has a reader}) \) by \( \bar{\rho}_i^r(t) := \langle r_i(t) \rangle \), where \( r_i(t) \in \{0, 1\} \) is the reader occupancy at site \( i \) at time \( t \), and the operator \( \langle \rangle \) denotes an average over the ensemble. This yields
\[
J_{i\rightarrow i+1}(t) = \gamma_i \bar{\rho}_i^r(t) \left( 1 - \sum_{k=0}^{\ell-1} \bar{\rho}_{i+\ell-k}^r(t) \right).
\]
\tag{A.19}

\footnote{Note that in [2] the reader is defined to be in the right-most site of the object, and thus there the current is proportional to the probability that site \( i \) has a reader and site \( i + 1 \) is empty.}
The change in the average reader occupancy at site $i$ at time $t$ is given by [2]:

$$
\frac{d}{dt} \rho^r_i(t) = J_{i-1 \rightarrow i}(t) - J_{i \rightarrow i+1}(t).
$$

(A.20)

Introducing the notation $x_i(t) := \rho^r_i(t)$ and $\lambda_i := \gamma_i$, we see that $J_{i \rightarrow i+1}(t)$ corresponds to $q_i(x)$ in (7), and (A.20) corresponds to (6) (see (4)). Thus, we obtained the RFMEO. In particular, the case $\ell = 1$ in (A.19) corresponds to the dynamical equations of the RFM (see (3)).

At steady-state, we expect every $\rho^r_i(t)$ in TASEPEO to converge to, say, $\bar{\rho}^r_i$, and then the currents between any two consecutive sites are all equal (but we are not aware of any rigorous proof of convergence in TASEPEO). The derivation above (including the boundary cases as well [3], [1]) shows that the steady-state current satisfies:

$$
J = \alpha (1 - \sum_{k=0}^{\ell-1} \rho^r_{\ell-k})
$$

$$
= \gamma_i \rho^r_i (1 - \sum_{k=0}^{\ell-1} \rho^r_{i+k})
$$

for all $1 \leq i \leq N - \ell$

$$
= \gamma_i \rho^r_i
$$

for all $N - \ell + 1 \leq i \leq N - 1$

(A.21)

If we use the notation $e_i := \rho^r_i$, $\lambda_0 := \alpha$, and $\lambda_n := \beta$ then this is just the steady-state equation of RFMEO given in (19).

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