Power spectra of a constrained totally asymmetric simple exclusion process

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Abstract. In nature, all biological systems function in a far-from-equilibrium state. Here, we study the process of translation in protein synthesis, using the totally asymmetric simple exclusion process (TASEP) as a model. In particular, we explore the effects of a finite supply of particles for the TASEP, as in a living cell with a finite pool of ribosomes. Specifically, we investigate the power spectrum associated with total occupancy, utilizing both Monte Carlo simulations and theoretical analysis. New features arise, such as large suppressions at low frequencies, due to the added constraint. A theory is formulated based on a Langevin approach with discrete space and time. With good agreement between the simulation and theory, we gain some insights into the effects of finite resources on the TASEP.

Keywords: driven diffusive systems (theory), stochastic processes (theory)
1. **Introduction**

The connection between the microscopic and macroscopic worlds via equilibrium statistical mechanics is one of the great achievements of the last century. However, systems that are far from equilibrium are still quite poorly understood. Even for non-equilibrium systems in time independent steady states, we do not have a comprehensive framework for providing the distribution of states. This lack of a distribution is in contrast to the case for the Boltzmann distribution, which appears to be valid for all equilibrium systems. However, many systems in nature, from biological systems to social networks, are not in equilibrium. One way to gain insight into the physics of such systems is to study simple models, on which more realistic and complex theories can be built.

One such simple non-equilibrium system is the totally asymmetric simple exclusion process (TASEP) [1]–[4]. Two kinds of boundary conditions are typically studied: periodic and open. With periodic boundary conditions, the stationary distribution is flat [2]. However, its dynamics differs from that of simple diffusion [5]. For the open TASEP, nontrivial behaviors are present, even for the steady state. There, depending on the entry and exit rates of particles at the boundaries, three distinct phases appear [6]—a half-filled phase with maximal current and high/low density phases. The exact analytical solution for the stationary distribution is known [7]–[9]. Many aspects of the richer and more complex dynamic properties of the TASEP are also established [10]–[12]. The understanding of these properties will be useful not only for attempts at setting up a general framework for non-equilibrium statistical mechanics, but also for potential applications to real systems.

In particular, the TASEP has been used to model biological transport [1,13,14], traffic flow [15], and surface growth [16].

The first appearance of the TASEP is as a model for the translation process during protein synthesis [1], where particles play the role of ribosomes that move along a discrete
chain of codons (the mRNA). In a cell, the number of ribosomes is clearly finite, in contrast to the case of the unlimited number of particles available to an open TASEP [2]–[4]. The effects of having finite resources on a TASEP were investigated recently [17,18], showing a few novel phenomena associated with its stationary states. In this paper, we explore the dynamical properties of this ‘constrained’ TASEP, examining the power spectrum associated with the total particle occupancy. This quantity has been previously studied for the unconstrained (ordinary) TASEP [19]: the power spectrum was found to display simple algebraic decays in the maximal current phase and oscillation at low frequencies in the high/low density phases. The oscillations were explained using a linearized Langevin equation in the continuum limit, though puzzling features of some of the fitting parameters remain unresolved [19]. Here, we present a systematic study of the problem. With improvements in several aspects, our theory provides substantially better agreement with data, with no fit parameters. Turning to the effects on finite resources, we extended the Monte Carlo investigations reported earlier [20], as well as the theory, to include the recycling of particles. How low frequency fluctuations are suppressed is well understood in terms of this approach and most of the data compare well with our predictions (again, without any fit parameters).

This paper is organized as follows. The section 2 introduces our model. In section 3, we present our Monte Carlo simulation results for the power spectra. Section 4 provides a theoretical explanation, based also on the linearized Langevin equation. In addition to incorporating the constraint due to finite resources, we improve on the previous approach [19] by using discrete space/time. Thus, fewer ambiguities are present when we compare these predictions with simulation results. With discrete time, we can implement a second improvement which involves the summing over harmonics, so a careful comparison with the simulation data is meaningful. Section 5 contains a summary and outlook.

2. Model

The original, unconstrained TASEP consists of particles moving unidirectionally on a one-dimensional lattice of \(L\) sites. These sites are labeled with \(x \in [1,L]\), and can be occupied by at most one particle. With open boundaries, particles may enter at (exit from) site 1 (\(L\)). For the convenience of an updating scheme, a ‘virtual’ site is included and labeled here as \(x = 0\). Representing the particle reservoir, its occupation is unconstrained (and irrelevant). In each Monte Carlo step (MCS), \(L+1\) sites are randomly chosen for updating. If the virtual site is chosen and the first site (\(x = 1\)) is vacant, then a particle enters the lattice with probability \(\alpha\). If the last site (\(x = L\)) is chosen and it is occupied, then the particle is removed with probability \(\beta\). For all other sites (\(x \in [1,L-1]\)), if occupied, the particle will be moved to the next site (\(x + 1\)), provided the latter is empty. Clearly, the total particle occupancy of the lattice, \(N(t)\), is fluctuating in time. In the steady state, \(N/L\) fluctuates around the constant overall density, \(\bar{\rho}\). The three phases in this state are characterized by: (i) maximal current (MC) with \(\bar{\rho} = 1/2\) for \(\alpha, \beta \geq 1/2\), (ii) high density (HD) with \(\bar{\rho} = 1 - \beta\) for \(\beta < 1/2\) and \(\alpha > \beta\), and (iii) low density (LD) with \(\bar{\rho} = \alpha\) for \(\alpha < 1/2\) and \(\alpha < \beta\). Along the boundary between the LD and HD phases (\(\alpha = \beta < 1/2\)), the systems display a LD region (at smaller \(x\)) coexisting with a HD one (at larger \(x\)), separated by a ‘shock’ or domain wall (DW) of microscopic width. The DW performs a random walk along the entire lattice causing large deviations in \(N(t)\). However in the...
long time limit, the average $\langle N \rangle / L$ approaches $1/2$. This coexistence boundary is often referred to as the ‘shock phase’ (SP).

For the constrained TASEP [17], the lattice is connected to a finite reservoir of particles. When particles enter (leave) the lattice, they are extracted from (recycled back into) this ‘pool’. Thus, it models the ribosomes in the cell that are not bound to the mRNA. Denoting the occupation in this pool by $N_p$, we consider a system with a fixed

$$N_{\text{tot}} = N + N_p.$$  

(1)

(In a real cell, ribosomes are constantly synthesized and degrade, so $N_{\text{tot}}$ is also fluctuating. But, for simplicity, we ignore this aspect here.) Physically, it is reasonable to assume that the rate for a ribosome in the pool binding to the mRNA should, in the limit of large $N_p$, approaches some fixed constant (from the details of the initiation process), which we denote by $\alpha$. On the other hand, this rate must vanish when $N_p$ is zero. This leads us to an $N_p$ dependent, effective entry rate $\alpha_{\text{eff}}$. We follow the convenient choice used in previous studies [17,18]:

$$\alpha_{\text{eff}}(N_p) = \alpha \tanh \left( \frac{N_p}{N^*} \right)$$  

(2)

where the crossover scale $N^*$ is typically chosen to be $\bar{\rho}L$. Interesting results have been reported, concerning how such a constraint affects the overall density and the current [17], as well as the density profile [18]. Here, we are interested in $I(f)$, the power spectrum associated with the total particle occupancy. In addition to providing information on the $t$ dependent fluctuations of $N(t)$, $I(f)$ reflects the correlations of the entry and exit currents and so reveals much about the dynamics of the system as a whole.

To be specific, we carry out many independent runs, record $N(t); t \in [1,T]$ for each, and compute the Fourier transform

$$\tilde{N}(f) = \frac{1}{T} \sum_{t=0}^{T} e^{i ft} N(t)$$  

(3)

with

$$f = \frac{2 \pi m}{T}; \quad m = 1, 2, \ldots .$$  

(4)

The power spectrum is defined as [19]:

$$I(f) = \langle |\tilde{N}(f)|^2 \rangle$$  

(5)

where the $\langle \ldots \rangle$ indicate the average over the many runs.

In the Monte Carlo simulations, a single Monte Carlo step (MCS) is defined as $L+1$ site updates. The system is allowed to reach the steady state by typically discarding the first $100k$ MCS. At the steady state, $N(t)$ is measured every 100 MCS for typically 1M MCS. Thus, we have $T = 10000$ measurements per run. For $I(f)$, we typically average $|\tilde{N}(f)|^2$ over 100 runs.

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Figure 1. Comparison of the power spectra of the ordinary and constrained TASEPs in the LD phase. The parameters for the former are \( \alpha = 0.1, \beta = 0.9 \); and for the latter: \( \alpha = 0.3, \beta = 0.9, N^* = 300, \) and \( N_{\text{tot}} = 205. \) With \( L = 1000, \) the two systems have the same average overall density: \( \bar{\rho} = 0.1. \)

3. Simulation results

In this section, we present our Monte Carlo simulation results. The ordinary TASEP settles into one of four states (LD, HD, SP, MC) depending on the \( \alpha \) and \( \beta \) chosen. For the constrained TASEP, we also have \( N_{\text{tot}} \) as an additional control parameter. The effects of \( N_{\text{tot}} \) on the average overall density (\( \bar{\rho} \)) and current (\( J \)) are studied in [17]. For small \( N_{\text{tot}} \), the system settles into an LD state, regardless of (\( \alpha, \beta \)). We will focus on this regime first.

3.1. Spectra in the LD regime

In the LD state of the ordinary TASEP, the power spectrum (denoted by \( I_o \)) displays damped oscillations at low frequencies [19]. Turning to the constrained TASEP with small \( N_{\text{tot}} \), we see similar oscillations for its power spectrum (denoted by \( I_c \)). To make a meaningful comparison between \( I_o \) and \( I_c \), we must choose systems having the same size (\( L \)) and average density (\( \bar{\rho} \)). Figure 1 illustrates such a comparison, for \( L = 1000 \) and \( \bar{\rho} = 0.1. \) While the differences vanish for large frequencies, \( I_c \) is seriously suppressed for \( m \lesssim O(10) \), i.e., the \( f \to 0 \) limit. To understand this behavior, consider the different timescales involved. On short timescales, fluctuations in \( N(t) \) do not have time to traverse the entire lattice (i.e., \( L/v = L/(1 - 2\bar{\rho}) \) [19]), which is necessary to provide the feedback. Since the feedback enters only through \( \alpha_{\text{eff}} \), such changes will not be seen on this timescale, so the two spectra are essentially identical. For larger timescales, the feedback will clearly affect the constrained TASEP and tends to ‘stabilize’ the numbers around its average. Thus, \( \alpha_{\text{eff}} \) suppresses the fluctuations in \( N(t) \). Specifically, the controlling factor
should be
\[ \alpha'_{\text{eff}} \equiv \partial_{N_p} \alpha_{\text{eff}} |_{N_p = \bar{N}_p} \]  
where \( \bar{N}_p = N_{\text{tot}} - \bar{\rho}L \) is the average occupation in the pool. To explore this idea, we exploit the freedom associated with different values of \( N^* \). While keeping the same \( \alpha \), we can simulate systems with a range of \( \alpha'_{\text{eff}} \). Of course, a meaningful comparison must keep the overall \( \bar{\rho} \) the same as well, so as to ensure that the locations of the minima in the power spectra remain unchanged. These conditions can be achieved easily by selecting the appropriate \( N_{\text{tot}} \):

\[ N_{\text{tot}} = \bar{\rho}L + N^* \tanh^{-1} (\bar{\rho}/\alpha) \]  
which originates from the equation [17] \( \bar{\rho} = \alpha_{\text{eff}} \). The results are shown in figure 2 for \( N^* = 30, 150, 300, 600 \) (\( \alpha'_{\text{eff}} = 8.9 \times 10^{-3}, 1.8 \times 10^{-3}, 8.9 \times 10^{-4}, 4.4 \times 10^{-4} \)), confirming these theoretical ideas.

Note that, since the feedback is expected to affect the lower frequency properties more, the suppression not only becomes larger near \( m = 0 \) as \( \alpha'_{\text{eff}} \) increases, but also begins to be noticeable for the higher frequencies as well. For the most extreme case shown here (\( \alpha'_{\text{eff}} = 8.9 \times 10^{-3} \)), we see that \( I_c \) begins to merge into \( I_0 \) only after \( m \sim 4000 \), as opposed to \( \sim 1200 \) in the three cases with smaller \( \alpha'_{\text{eff}} \).

Finally, the period of the oscillations is governed by the time that it takes for fluctuations to traverse the lattice [19]. In particular, the \( m \) value of the first minimum is proportional to \( L^{-1} \), for both \( I_0 \) and \( I_c \). An example of how these spectra compare is shown in figure 3, using a relatively small \( \alpha'_{\text{eff}} = 2.78 \times 10^{-5} \) and a much larger \( L = 32000 \).

### 3.2. Spectra in the SP-like regime

Next, we consider setting \( \alpha \) and \( \beta \) such that the ordinary TASEP would be in the HD phase. This choice leads to a new regime for the constrained system as \( N_{\text{tot}} \)
Figure 3. Comparison of the power spectra of the ordinary and constrained TASEPs in the LD phase. The parameters for the former are $\alpha = 0.1$, $\beta = 0.9$; and for the latter: $\alpha = 0.3$, $\beta = 0.9$, $N^* = 9600$, and $N_{\text{tot}} = 6527$. With $L = 32000$, the two systems have the same average overall density: $\bar{\rho} = 0.1$.

is increased [17]. In this regime, changes in $N_{\text{tot}}$ are completely absorbed by the lattice, leaving $N_p$ essentially constant. It is characterized by the average of $\alpha_{\text{eff}}(N_p)$ taking the value $\beta$, so a shock (domain wall, DW [21]) is present in the lattice, i.e., it is comparable to the SP in an ordinary TASEP. The major difference between this constrained case and the unconstrained case is that the DW is relatively localized [18], rather than performing a random walk through the entire lattice. As a result, the power spectrum is modified, from $I_o \propto f^{-2}$ to $I_c \propto (f^2 + \gamma^2)^{-1}$, showing again the expected suppression at small frequencies. Figure 4 shows a good example of this phenomenon, with $L = 1000$, $\alpha = 0.7$, $\beta = 0.3$, $N^* = 700$, and $N_{\text{tot}} = 800$.

Although the constraint is responsible for the suppression of all power spectra, the detailed mechanism is subtly different from the LD case. There, fluctuations in the lattice take a characteristic time to traverse the lattice ($L/v$) and then feed back to the entry rate, $\alpha_{\text{eff}}$, through $N_p = N_{\text{tot}} - N$. In the SP-like regime, a fluctuation can be just ‘absorbed’ by the shock, so both $N_p$ and $\alpha_{\text{eff}}$ are essentially independent of $N$ (or $N_{\text{tot}}$), with $\alpha_{\text{eff}} \approx \beta$. Of course, $\alpha'_{\text{eff}}$ still plays a role. But, since

$$\partial N_p \alpha_{\text{eff}} = \frac{\alpha}{N^*} \left[ 1 - \tanh^2 \left( \frac{N_p}{N^*} \right) \right] = \frac{\alpha^2 - \alpha_{\text{eff}}^2}{\alpha N^*},$$

we find $\alpha'_{\text{eff}}$ to be adequately given by $(\alpha^2 - \beta^2)/(\alpha N^*)$, a quantity that does not depend explicitly on $N_{\text{tot}}$ or $L$. To verify this picture, we first tested the hypothesis that changing $N_{\text{tot}}$ in this regime does not affect the power spectrum. Indeed, as shown in figure 5(a), for $\alpha = 0.7$, $\beta = 0.3$, $N^* = 700$, and $N_{\text{tot}} = 700, 800, 900$, the simulation data for the various $I_c$ lie on top of each other. Similarly, we can compare $I_c$ for various values of $L$s, an example being provided by figure 5(b), where $\alpha, \beta, N^* = 0.7, 0.3, 700$ with $L = 1000, 2000, 5000, 10000$. We should re-emphasize that, for the unconstrained TASEP
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Figure 4. Comparison of the power spectra of the ordinary and constrained TASEPs in the SP-like regime, where the average $\alpha_{\text{eff}} = \beta$. Here, $L = 1000$ with $\alpha = 0.7$, $\beta = 0.3$, $N^* = 700$, and $N_{\text{tot}} = 800$ for the constrained TASEP, while $\alpha = \beta = 0.3$ for the ordinary TASEP.

on the SP line, $L$ appears simply as a crossover scale at low frequencies in $I_o(f)$, signifying the finite length of the system. Apart from this effect, the $I_o$ for different $L$ values collapse to a single $1/f^2$ curve. For the constrained case, the finite extent covered by the shock is controlled by the feedback [18]. Thus, the crossover scale is fixed, as long as $L$ is greater than this localization length (as is the case in the figure). More details of this theory are provided below.

We end this section with a brief comment on the other phases: HD, MC, and the true SP. These phases only occur at large $N_{\text{tot}}$, where $\alpha_{\text{eff}} \approx \alpha$. Since $\alpha_{\text{eff}}$ is almost constant as $N_{\text{tot}}$ changes, the feedback plays hardly any role and $I_c$ becomes indistinguishable from $I_o$ in the large $N_{\text{tot}}$ limit for all $\alpha$ and $\beta$.

4. Theoretical analysis

In this section, we present a Langevin approach to understanding $I_c$, the power spectrum of the constrained TASEP. Since the power spectrum contains information about time correlations, it cannot be obtained from the stationary distribution. In principle, it can be computed from the full solution of the master equation. However, even if all the eigenvalues and eigenvectors are known (as in the case of the ordinary TASEP [11]), the power spectrum requires the evaluation of complicated matrix elements as well as a sum over all the eigenvalues/vectors [22]. Thus, finding an exact answer, even for $I_o$, is impossible at present. Instead, we will use a phenomenological approach, exploiting the Langevin equation. Here, we will only consider a linearized version, as in [19]. However, our approach (for the LD case) differs in four important aspects. First, we use discrete space and time variables rather than continuous ones, so UV cutoffs are automatically
Figure 5. Comparison of the power spectra of the constrained TASEP when the average $\alpha_{\text{eff}} = \beta$ with (a) $L = 1000$ for various $N_{\text{tot}}$ values and (b) for various $L$ values.

incorporated. This provides a solid foundation for future studies using perturbation theory. Second, we formulate our TASEP on a ring of $L + 1$ sites, where the extra site is the pool, thereby avoiding issues with open boundaries. Of course, there is no restriction on the number of particles that occupy this extra site. Note also that, since $N(t) = N_{\text{tot}} - N_p(t)$, the power spectrum associated with $N(t)$ is identical to the one for $N_p(t)$ (apart from the uninteresting $f = 0$ component). Third, we choose our discrete time step to correspond to the smallest scale in the simulations, i.e., the update of each site. Since the measurements are taken every 100 MCS, the observed spectra must not be compared naively to the Fourier transform of the theoretical $N(t)$. Instead, we must sum over the appropriate harmonics of the latter first. As will be shown below, this action leads to substantial improvements in certain cases. Finally, the completely new feature here is an $N_p$ dependent entry rate, $\alpha_{\text{eff}}$. Linearization also means that $\alpha'_{\text{eff}}$ enters naturally, with no need to consider higher derivatives. As for the SP-like case, an entirely different approach is used, since the stationary density profile is not homogeneous. Instead, we exploit the domain wall (DW) description for the system [12, 19], since the position of the DW is directly related to $N(t)$. The crudest approximation leads to a linear Langevin equation for $N(t)$ and is shown to be entirely adequate for reproducing the data.

4.1. The LD regime

To gain insight into suppressing the power spectrum in the LD state better, we construct a theory that incorporates the feedback effects of $\alpha_{\text{eff}}$. Our starting point is a Langevin equation for the continuous variable, $\rho(x, t)$, the density of particles (in some statistically averaged sense). To follow simulations more closely, we will also use discrete space ($x \in [0, L]$) and discrete time, $\tau$, labeling each attempt at updating. Thus, $\tau = 1, 2, \ldots, M$, with

$$M \equiv \ell T; \quad \ell \equiv 100(L + 1) \quad (9)$$

and measurements are taken at $\tau = \ell t$, with $t = 1, \ldots, T$. 

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For ρ in the bulk of the lattice \((x = 2, \ldots, L - 1)\), we have
\[
\Delta \rho(x, \tau) \equiv \rho(x, \tau + 1) - \rho(x, \tau) = \frac{\rho(x - 1, \tau)[1 - \rho(x, \tau)] - \rho(x, \tau)[1 - \rho(x + 1, \tau)]}{L + 1} + \xi(x, \tau) - \xi(x - 1, \tau).
\] (10)

Here, the factor \(1/(L + 1)\) simply reflects that, on average, only one out of \((L + 1)\) sites is chosen for updating. In the last line, \(\xi(x, \tau)\) is assumed to be a homogeneous, uncorrelated white noise associated with the hop from site \(x\) to site \(x + 1\), with variance \(A\), i.e.,
\[
\langle \xi(x, \tau)\xi(x', \tau') \rangle = A\delta(x, x')\delta(\tau, \tau').
\] (11)

Although a good estimate for \(A\) can be gleaned from the microscopic dynamics [11,12], we will let it be a ‘fit parameter’ here (details below).

For the two boundary sites, we have
\[
\Delta \rho(1, \tau) = \alpha_{\text{eff}}[1 - \rho(1, \tau)] - \rho(1, \tau) + \xi(0, \tau) - \xi(1, \tau)
\] (12)
\[
\Delta \rho(L, \tau) = \frac{\rho(L - 1, \tau)[1 - \rho(L, \tau)] - \beta\rho(L, \tau)}{L + 1} + \xi(L - 1, \tau) - \xi(L, \tau)
\] (13)

and for the pool \((x = 0)\), we write
\[
\Delta \rho(0, \tau) = \frac{\beta\rho(L, \tau) - \alpha_{\text{eff}}[1 - \rho(1, \tau)]}{L + 1} + \xi(L, \tau) - \xi(0, \tau).
\] (14)

Of course, being a continuum version of \(N_p(\tau)\), \(\rho(0, \tau)\) can exceed unity while all other \(\rho\)s may not. Note that the only way \(\rho(0, \tau)\) enters into these equations is through \(\alpha_{\text{eff}}\). Thus, in an ordinary TASEP, \(\rho(0, \tau)\) is entirely irrelevant to the dynamics. Let us re-emphasize that we regard our system as a complete ring of \(L + 1\) sites, so Fourier transforms on a periodic lattice can be exploited.

To simplify the remaining parts of the calculation, we choose \(\alpha\) and \(\beta\) such that the average density profile is homogeneous, i.e.,
\[
\rho(x) = \bar{\rho}; \quad \bar{N} = \bar{\rho}L \quad \bar{\alpha}_{\text{eff}} = \bar{\rho}; \quad \beta = 1 - \bar{\rho}
\] (15)

where
\[
\bar{\alpha}_{\text{eff}} \equiv \alpha_{\text{eff}}(\bar{N}_p) \quad \text{with} \quad \bar{N}_p = N_{\text{tot}} - \bar{\rho}L
\] (16)

is just the average entry rate. In practice, once we fix \(\alpha, \beta, N^*\), this simply means that we set \(N_{\text{tot}}\) in order for these conditions to be satisfied, i.e.,
\[
N_{\text{tot}} = (1 - \beta) L + N^* \tanh^{-1} \left( \frac{1 - \beta}{\alpha} \right)
\] (17)

explicitly. Next, define the fluctuation of \(\rho(x, \tau)\) about its average \(\bar{\rho}\) to be
\[
\varphi(x, \tau) = \rho(x, \tau) - \bar{\rho}; \quad x \in [1, L]
\] (18)

and similarly for the pool:
\[
\varphi(0, \tau) = \rho(0, \tau) - \bar{N}_p.
\] (19)
At low densities, the interparticle spacing should be sufficiently large that (the excluded volume) interactions do not contribute significantly. These interactions are incorporated in the Langevin equation above in the form of \( \rho(1 - \rho) \), and so, as terms quadratic in \( \varphi \). Since we assume that the fluctuations of \( \rho \) about \( \bar{\rho} \) are small, we drop such quadratic terms in the following. Studying their effects on the system by using systematic perturbation theory can reveal interesting aspects of the exclusion process [23] and this will be presented elsewhere.

Proceeding to linearize the equations, we should keep in mind that \( \alpha_{\text{eff}} \) depends on the pool occupation \( \rho(0, \tau) \), and so, we will need

\[
\alpha_{\text{eff}} = \bar{\alpha}_{\text{eff}} + (\rho(0, \tau) - \bar{N}_p) \alpha'_{\text{eff}} + \cdots
\]

The result is

\[
\Delta \varphi(0, \tau) = \frac{(1 - \bar{\rho})\varphi(L, \tau) - (1 - \bar{\rho})\varphi(0, \tau)\alpha'_{\text{eff}} + \bar{\rho}\varphi(1, \tau)}{L + 1} + \cdots
\]

\[
\Delta \varphi(1, \tau) = \frac{(1 - \bar{\rho})\varphi(0, \tau)\alpha'_{\text{eff}} - \varphi(1, \tau) + \bar{\rho}\varphi(2, \tau)}{L + 1} + \cdots
\]

\[
\Delta \varphi(x, \tau) = \frac{(1 - \bar{\rho})\varphi(x - 1, \tau) - \varphi(x, \tau) + \bar{\rho}\varphi(x + 1, \tau)}{L + 1} + \cdots
\]

\[
\Delta \varphi(L, \tau) = \frac{(1 - \bar{\rho})\varphi(L - 1, \tau) - \varphi(L, \tau)}{L + 1} + \cdots
\]

where \( + \cdots \) denotes the noise terms. Since most of the equations of this set satisfy translational invariance, it is convenient to write the entire set as

\[
\Delta \varphi(x, \tau) = \frac{1}{L + 1} \{(1 - \bar{\rho})\varphi(x - 1, \tau) - \varphi(x, \tau) + \bar{\rho}\varphi(x + 1, \tau)
\]

\[
+ \varphi(0, \tau)[(1 - (1 - \bar{\rho})\alpha'_{\text{eff}})\delta_{x,0} + (1 - \bar{\rho}) (\alpha'_{\text{eff}} - 1) \delta_{x,1} - \bar{\rho}\delta_{x,L}]\} + \cdots. \quad (22)
\]

In this form, our equation exposes that the translational invariance of the ring is broken only by the rules associated with the \( x = 0 \) site, and so, the second and third lines depend only on \( \varphi(0, \tau) \). Using Fourier transforms, a straightforward though tedious computation (details provided in the appendix) leads to the solution

\[
\varphi(x, \tau) = \sum_{k, \omega} e^{i(kx - \omega \tau)} \tilde{\varphi}(k, \omega)
\]

with

\[
\tilde{\varphi}(k, \omega) = \frac{(e^{-ik} - 1) \tilde{\xi}(k, \omega)}{P(k, \omega)} + \frac{g(k)}{Q(\omega)P(k, \omega)} \sum_{q} \frac{(e^{-iq} - 1) \tilde{\xi}(q, \omega)}{(L + 1)P(q, \omega)}. \quad (24)
\]

Here, \( g \) is defined in equation (A.7) and

\[
P(k, \omega) = e^{i\omega} - 1 + \frac{(1 - \cos k) + iv \sin k}{L + 1} \quad \text{with} \quad v \equiv 1 - 2\bar{\rho} \quad (25)
\]

\[
Q(\omega) = \frac{1}{L + 1} \sum_{q} \frac{(L + 1)(e^{i\omega} - 1) + \alpha'_{\text{eff}}(1 - \bar{\rho})(1 - e^{-iq})}{(L + 1)(e^{i\omega} - 1) + (1 - \cos q) + iv \sin q}. \quad (26)
\]
Now, our interest is $I(f)$ which can be obtained from the power spectrum

$$I(\omega) = \langle |\tilde{N}(\omega)|^2 \rangle.$$  

By exploiting $N(\tau) = N_{\text{tot}} - N_0(\tau)$, we see that $I(\omega) = \langle |\tilde{N}_0(\omega)|^2 \rangle$ for $\omega \neq 0$. Thus, we only need $\varphi(0, \tau)$ and its Fourier transform, $(L + 1)\sigma(\omega)$, as defined in equation (A.6). Explicitly, we have

$$(L + 1)\sigma(\omega) = \sum_q \left( \frac{e^{-iq} - 1}{Q(\omega)P(q, \omega)} \right)$$  \hspace{1cm} (28)

from equation (A.10), and using equation (11), we obtain

$$I(\omega) = \frac{2A}{(L + 1)T|Q(\omega)|^2} \sum_k \frac{1 - \cos k}{|P(k, \omega)|^2}.$$  \hspace{1cm} (29)

Before exploring the various consequences of this result, let us discuss the only unknown in this formula: $A$. Although it can be treated as a ‘free’ fit parameter for normalizing $I(\omega)$, we will exploit the sum rule. $I(\omega)$ is just the Fourier transform of the autocorrelation $\langle N(t)N(t') \rangle$, so $\sum_{\omega=0} I(\omega) \propto \langle N^2(t) \rangle$ in the steady state. For the ordinary TASEP, $\langle N^2(t) \rangle$ is known exactly, and so, we have zero-parameter fits for those cases. For the constrained case, we will use the time series $N(t)$ from simulations to compute the fluctuations

$$(\Delta N)^2 \equiv \left\langle \left[ N(t) - \tilde{N} \right]^2 \right\rangle.$$  \hspace{1cm} (30)

When comparing theory with data below, we will fix $A$ through this condition.

Returning to equation (29), we may set $\alpha_{\text{eff}}' = 0$ to retrieve the power spectrum for an ordinary TASEP: $I_o(\omega)$. Since its appearance is quite different from the result in [19]

$$I_{\text{ASZ}}(\omega) \propto \int_k \left| \frac{e^{ikL} - 1}{Dk^2 + ik - i\omega} \right|^2$$  \hspace{1cm} (31)

we find it worthwhile to compare the two first, and then to discuss how our approach is better at predicting the simulation data. Examining equations (29) and (31), we readily identify the same key elements—oscillations due to $\omega - vk$ and damping from $k^2$—and may expect similar results. To be quantitative, we evaluated both expressions numerically for $L = 1000$ and $\alpha = 1 - \beta = 0.1$ (while normalizing both to be equal in the $\omega \to 0$ limit). The differences are less than 3%. Thus, our conclusion is that the two approaches—ours with discrete space–time and a careful account for the boundary conditions versus the naive approach in [19] with a ‘bare’ $D = 1/2$—yield essentially the same power spectra: $I_o(\omega) \simeq I_{\text{ASZ}}(\omega)$.

As noted in [19], a good fit to the data can be achieved only with serious ‘renormalization’ of the diffusion coefficient $D$. In the inset of figure 6, we illustrate with the case $L = 1000$ and $\alpha = 1 - \beta = 0.1$, showing the improvement that $I_{\text{ASZ}}(\omega; D = 2.8)$ provides over $I_{\text{ASZ}}(\omega; D = 1/2)$. Note that, while the small $\omega$ region is well fitted, the theory drops well below the data. Since our $I_o(\omega)$ differs little from $I_{\text{ASZ}}(\omega; D = 1/2)$, our efforts may appear to be in vain. On closer examination, however, we find another important aspect that was missed in $I_{\text{ASZ}}$. Since the simulation only recorded data every
Figure 6. Power spectra comparison of the theoretical and simulation results of the ordinary TASEP with $L = 1000$ for $\alpha = 1 - \beta = 0.1$. The main figure shows the improvement of this theory (with no free parameters) over the one in [19] (with two fitted parameters). The inset shows the effect of 'renormalizing' the effective diffusion coefficient [19].

$\ell$ updates (every 100 MCS), $I(\omega = 2\pi n/M)$ should not be directly compared to the measured $I(f = 2\pi m/T)$. The difference between the two lies in a straightforward sum over the $T/\ell$ harmonics of $f$. Our final result, written in terms of $m$ for easy comparison with data, is

$$I(m) = \sum_{j=0}^{\ell-1} \sum_{k} \frac{2A(1 - \cos k)}{(L + 1)T|Q(\omega_{m,j})P(k, \omega_{m,j})|^2}$$

(32)

where

$$\omega_{m,j} = \frac{2\pi m}{T} \left(1 + j \frac{T}{\ell}\right) = \frac{2\pi}{M} (m\ell + jT).$$

(33)

Note that equation (32) still contains $A$. It will be fixed, for all comparisons with data, by the sum rule discussed above. To be precise, we impose

$$A = \frac{\sum_{m=1}^{T-1} I(m)}{(\Delta N)^2}$$

(34)

with the measured $(\Delta N)^2$. Only in this sense is $A$ a ‘fit parameter’. Let us turn to the data next and see what this theory predicts.

First, we show in the main part of figure 6 the effect of the harmonic sum. Unlike the two $I_{\text{ASZ}}$ (inset), we find that our $I(m)$ fits the large $\omega$ region quite well. Of course, our $I(m)$ still offers no resolution for the enhanced damping of the oscillations. Nevertheless, we are hopeful that, once the problem of $D$-renormalization is understood, the agreement
between theory and simulations of the ordinary TASEP will be irreproachable. In the remainder of this paper, we will not introduce $D$ as an ad hoc parameter, especially since it is not obvious where to insert such a quantity into our expressions.

Next, we investigate the effects of the constraint. To find $I_c(m)$, the only change needed is to set $\alpha'_\text{eff}$ to be the appropriate value in $Q$ (in equation (26)) and insert that into equation (32). Comparing such a prediction with the simulation results, we find that the suppression at low $f$ is accurately captured by this theory. Not surprisingly, $I_c(m)$ has the same defect as $I_o(m)$, namely, insufficient damping of the oscillations. Illustrations of these findings are shown in figures 7 and 8, both with $L = 1000$ and $\alpha = 0.3$, $\beta = 0.9$. In the former, we choose $N_{\text{tot}} = 205$ and $N^* = 300$ so that we have $\bar{\alpha} \approx 0.1$ and a moderate $\alpha'_\text{eff} \approx 8.9 \times 10^{-4}$. In the latter, we have $N_{\text{tot}} = 110$ and $N^* = 30$, giving also $\alpha \approx 0.1$ but a much larger $\alpha'_\text{eff} \approx 8.9 \times 10^{-3}$. Other than missing the peaks and valleys, the agreement between theory and simulations is again excellent.

Since our predictions for both the ordinary and the constrained TASEP share a similar deficiency (underdamped oscillations), it is reasonable to consider the ratio of these power spectra: $I_o/I_c$. If the agreement is good for the ratio, then we may conclude that the approach for incorporating the constraint is successful. Further, we can expect that future improvements for the ordinary TASEP would also help in the constrained case. From equation (32), we see that the only factor affected by the constraint (i.e., the one with $\alpha'_\text{eff}$) is in $Q$. Defining $Q_0$ as $Q$ with $\alpha'_\text{eff} = 0$, we easily obtain

\begin{equation}
\frac{I_o(m)}{I_c(m)} = \frac{\sum_j |Q(\omega_{m,j})|^2}{\sum_j |Q_0(\omega_{m,j})|^2}
\end{equation}

an expression far simpler than each of the individual spectra. Of course, a meaningful ratio should involve TASEPs with the same $L$ and average density $\bar{\rho}$. These ensure the $v$s and the positions of the minima to be the same. Further, the dependence on $A$ will

![Comparison of the power spectra of the simulation and theory for the constrained TASEP with $L = 1000$, $\alpha = 0.3$, $\beta = 0.9$, $N_{\text{tot}} = 205$, and $N^* = 300$.](image-url)
Figure 8. Comparison of the power spectra of the simulation and theory for the constrained TASEP with $L = 1000$, $\alpha = 0.3$, $\beta = 0.9$, $N_{\text{tot}} = 110$, and $N^* = 30$.

also be equal, so the theoretical ratio is entirely free of fit parameters! Comparing this prediction with the data, we find surprisingly good agreement, over the entire range of $m$. In figures 9 and 10, we show the ratios corresponding to the power spectra in figures 7 and 8 of $L = 1000$ with $\bar{\rho} = 0.1$ for $N^* = 300$ and $N^* = 30$, respectively. It is reasonable to conclude that our approach for accounting for the effects of the constraint is completely successful. The only remaining hurdle for a complete theory is a good understanding of the sizable ‘renormalization’ of the damping.

4.2. The SP-like regime

Turning our attention to the SP-like regime, we first recall that, for the ordinary TASEP in SP, $N(t)$ performs an unbiased random walk (with reflecting boundaries at $\alpha L$ and $(1 - \alpha)L$). An excellent interpretation is that the shock (DW) performs such a walk within the lattice. Good agreement with simulations can be obtained using a master equation for the position of the DW [21], and so $I_o(f)$ displays a $1/f^2$ power law decay (in the continuous time limit) [19, 12]. Following these ideas, a good description for the constrained TASEP is given in terms of a diffusing DW with position dependent hopping rates [18]. In particular, the feedback plays a central role in localizing the DW [18]. The physics of this picture strongly suggests that density fluctuations do not travel down the lattice with a well defined average, but instead, they get absorbed by the shock. If so, then we can account for the fluctuations in $N$ through the noise in the currents at the two ends. An adequate description of such a scenario can be formulated with a simple Langevin equation for $\delta N(t)$, the deviation of $N(t)$ from its average, $\bar{N}$. In the continuous time limit, this reads

$$\frac{\partial}{\partial t} \delta N(t) = -\gamma \delta N(t) + \xi(0, t) - \xi(L, t)$$

(36)
where $\gamma$ represents the feedback-induced restoration. To find $\gamma$, we begin with

$$
\partial_t N(t) = J(0, t) + \xi(0, t) - J(L, t) - \xi(L, t)
$$

(37)

where the currents at the entry/exit sites are given on the right. In SP, the (deterministic part of the) currents do not depend on density, but only $\alpha$ and $\beta$. Thus, we write

$$
J(0) = \alpha_{\text{eff}}(1 - \alpha_{\text{eff}}); \quad J(L) = \beta(1 - \beta)
$$

(38)
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Figure 11. Comparison of the power spectra of the simulation and theory for the constrained TASEP with $L = 1000$, $\alpha = 0.7$, $\beta = 0.3$, $N_{\text{tot}} = 800$, and $N^* = 700$.

for our case. Expanding $\alpha_{\text{eff}}(N_p(t)) = \alpha_{\text{eff}}(N_{\text{tot}} - N(t))$ about $\bar{N}$, we have

$$\alpha_{\text{eff}} = \bar{\alpha}_{\text{eff}} - \delta N(t)\alpha'_{\text{eff}} + \cdots \quad (39)$$

and so

$$\alpha_{\text{eff}} = \bar{\alpha}_{\text{eff}} - \delta N(t)\alpha'_{\text{eff}} + \cdots$$

In order to observe SP in a constrained TASEP, we must have $\bar{\alpha}_{\text{eff}} = \beta$. Thus, we conclude that

$$\gamma = (1 - 2\beta)\alpha'_{\text{eff}} \quad (41)$$

The solution to equation (37) is trivial: $\tilde{N}(\omega) = [\tilde{\xi}(L, \omega) - \tilde{\xi}(0, \omega)]/(i\omega + \gamma)$ and the power spectrum follows readily:

$$I_{\text{SP}}(\omega) = \frac{2A}{\omega^2 + \gamma^2} \quad (42)$$

Significantly, unlike for the case of an ordinary (finite) TASEP, this expression is $L$ independent. Of course, this property can be traced to the DW being localized to a distance controlled by $\alpha'_{\text{eff}}$ rather than $L$. Thus, for large enough $L$, the power spectrum is characterized only by this localization length, through $\gamma$.

Fixing $A$ with the sum rule, we again find excellent agreement between equation (42) and the simulation data. Figure 11 shows the results for $L = 1000$ with $\alpha = 0.7$, $\beta = 0.3$, $N_{\text{tot}} = 800$, and $N^* = 700$. In principle, we should carry out an analysis of harmonic sums similar to that for the LD case. However, in view of the good fit to data, this exercise seems unnecessary. For completeness, we also investigated the ratio of $I_o/I_c$ for the SP-like regime. Not surprisingly, the agreement between theory and data is also excellent, as illustrated in figure 12.

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5. Summary and outlook

In this paper, we investigated the effect of finite resources on the power spectra associated with $N$, the total occupancy of a TASEP. Particles leaving the lattice enter a pool and are recycled back onto the chain with $\alpha_{\text{eff}}$, a rate which depends on the numbers in the pool, $N_p$. Since the total number of particles is fixed, such a feedback on $N$ is expected to suppress the fluctuations. Using Monte Carlo simulations for both the LD state and SP-like regime, we do indeed find this effect, though mainly at the low frequencies. The rate of change of $\alpha_{\text{eff}}$ with respect to $N_p$ controls the level of suppression.

To understand this effect quantitatively, we proposed a phenomenological Langevin approach, in the same spirit as for the previous study for the ordinary TASEP [19]. For the LD cases that we considered, the average profile in the lattice is a constant ($\bar{\rho}$), so the Langevin equation for $\rho(x)$ can be linearized and the resultant for its deviations can be solved. In addition to incorporating the constraint, we have improved on [19] in several significant ways. (a) Using a description with discrete space–time, we automatically incorporate all the finite cutoff and finite system size effects. This forms a firm basis for future treatments of non-linearities by perturbation theory. (b) The introduction of a pool allows the entire system to be placed on a ring, thereby eliminating concerns associated with a proper accounting for the open boundaries. (c) Defining the discrete time step as the smallest one in simulations (a single update attempt), we are able to take into account the difference between the theoretical predictions for $I_\omega(\omega)$ and the $I_\omega(f)$ from simulations. Since the latter is formed from measuring $N$ every 100 MCS ($\ell$ updates), a harmonic sum over the former must be performed before quantitative comparisons are meaningful. (d) Exploiting the sum rule, we can fix the noise amplitude $A$, which was treated as a fit parameter in [19]. With these improvements, our theory for the LD case provides a better prediction (with no free fit parameters) for $I_\omega(f)$ over the entire range.

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of frequencies. Without introducing a ‘renormalized’ diffusion coefficient, our theory also fails to fit the (damped) amplitude of the oscillations completely, though it fails to a lesser degree than the previous approach [19]. Since the discrepancies are no longer large, we are hopeful that lowest order perturbation theory will provide a complete solution to this phenomenon.

Apart from under-predicting the damping, our theory of $I_c(f)$ also compares well with data for the constrained TASEP. Since we believe that the same mechanism for correcting the damping is at work for both $I_o(f)$ and $I_c(f)$, we considered the ratio $I_o/I_c$. It is gratifying that, with zero free parameters, our theoretical predictions lie well within the statistical errors of the simulation results.

For the SP regime, the average profile is inhomogeneous, with a delocalized shock in the ordinary TASEP [21] and a localized one in the constrained case [18]. Fluctuations, characterized by the position of the domain wall, are system-wide in the former. Due to the constraint, the DW is limited to a finite region and a meaningful average profile emerges [18]. However, linearizing the Langevin about such an average would lead to a nontrivial, Schrödinger-like, equation for the deviations. Instead, we proposed a simple approximation, in the spirit of the DW theory [21], i.e., a Langevin equation for $N(t)$, which can be related to the position of the shock. A much simpler analysis leads to theoretical spectra that agree with the data extremely well. Our conclusion is that this simple approach captures all the essential characteristics of the constrained TASEP in the SP regime.

While this study provided considerable closure for the problem of power spectra in these TASEPs, there is much room for further investigations. We end with describing just a few.

Though our expression ($I_o$ in equation (32)) led to a better fit for the ordinary TASEP power spectra than the previous one ($I_{ASZ}$, equation (31)), the latter is superior at highlighting the roles that $v, L, D$ played in predicting damped oscillations. By contrast, our expression is quite cumbersome. It would be useful to develop better insight into the various components hidden here. For example, taking the continuum limit carefully would be a logical and helpful next step.

Quantitative accounting for the enhanced damping remains to be performed. Starting from the results above, perturbation theory will not be straightforward, since equation (A.12) implies that the quadratic form (in a dynamic functional with these fields [24]) is not yet diagonal. Additional complications, due to the lack of translational invariance in the non-linearities, also present further challenges.

The original motivation for studying power spectra lies in understanding a certain aspect of protein synthesis within a living cell. There, the lattice corresponds to mRNA, sites model the codons, the particles represent the ribosomes and TASEP models the translation process. Many ingredients of life are missing in this model, three of which are as follows. (i) Ribosomes are large molecules and typically cover 10–12 codons, so TASEPs with extended objects are necessary. (ii) Codons in a real gene are different, and typically, the ribosome moves from one codon to the next with different rates, so TASEPs with inhomogeneous hopping rates would be more appropriate. (iii) Typically, there are thousands of different mRNAs, and many copies of each kind, in a cell competing for the same resources (pool of ribosomes). Therefore, having multiple TASEPs connected to a single pool of particles would model mRNA competition more closely. Incorporating

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these ingredients has serious consequences for the steady states of TASEP \[13, 25\]. How the first two would affect the power spectra is clearly of interest. More importantly, the power spectra of several, competing TASEPs can assist in answering ‘Who wins and who loses?’ Such cross-correlations should provide valuable insight into the time dependence of protein synthesis.

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Appendix. Details of solution for the power spectrum

To solve equation (22), we define Fourier transforms

\[
\varphi(x, \tau) = \sum_{k, \omega} e^{i(kx-\omega \tau)} \hat{\varphi}(k, \omega); \quad \xi(x, \tau) = \sum_{k, \omega} e^{i(kx-\omega \tau)} \hat{\xi}(k, \omega)
\]  

(A.1)

with

\[
k = \frac{2\pi \ell}{L + 1}; \quad \ell = 1, \ldots, L + 1
\]

(A.2)

\[
\omega = \frac{2\pi n}{M}; \quad n = 1, \ldots, M
\]

(A.3)

and inverse \( \hat{\varphi} = \sum_{x, \tau} e^{i(kx+\omega \tau)} \varphi/M(L + 1) \), etc. Treating the \( \varphi(0, \tau) \) term as an inhomogeneity (on the same footing as the noise in this linear equation), we write

\[
\sum_{k, \omega} e^{i(kx-\omega \tau)} P(k, \omega) \hat{\varphi}(k, \omega) = \frac{\varphi(0, \tau)}{L + 1} + \sum_{k, \omega} e^{i(kx+\omega \tau)} \left( e^{-ik} - 1 \right) \hat{\xi}(k, \omega)
\]

(A.4)

where \( P(k, \omega) \) is defined in equation (25):

\[
P(k, \omega) = e^{i\omega} - 1 + \frac{(1 - \cos k)}{L + 1} + iv \sin k \quad \text{L + 1}
\]

(A.5)

Note that the spatial and temporal parts of the inhomogeneity factorize, so it will be convenient to define

\[
\sigma(\omega) \equiv \frac{1}{M} \sum_{\tau} e^{i\omega \tau} \varphi(0, \tau)
\]

(A.6)

and

\[
g(k) \equiv \frac{1}{L + 1} \sum_{x} e^{-ikx} \left[ (1 - (1 - \bar{\rho})\alpha'_{\text{eff}}) \delta_{x,0} + (1 - \bar{\rho}) (\alpha'_{\text{eff}} - 1) \delta_{x,1} - \bar{\rho} \delta_{x,L} \right]
\]

\[
= \left[ 1 - \cos k + iv \sin k - \alpha'_{\text{eff}}(1 - \bar{\rho}) \left( 1 - e^{-ik} \right) \right] / (L + 1)
\]

(A.7)
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(where we exploited \( \exp[-i k (L + 1)] = 1 \)). Thus, the solution reads

\[
\tilde{\varphi}(k, \omega) = \frac{\sigma(\omega) g(k) + (e^{-ik} - 1) \tilde{\xi}(k, \omega)}{P(k, \omega)}.
\]

(A.8)

The only step remaining is to solve for \( \sigma(\omega) \). Using \( \varphi(0, \tau) = \sum q, \omega e^{-i \omega \tau} \tilde{\varphi}(q, \omega) \), we have

\[
\sigma(\omega) = \frac{1}{L + 1} \sum q \tilde{\varphi}(q, \omega)
= \sum q \frac{\sigma(\omega) g(q) + (e^{-iq} - 1) \tilde{\xi}(q, \omega)}{(L + 1) P(q, \omega)}
\]

(A.9)

and so

\[
\sigma(\omega) = \frac{1}{Q(\omega)} \sum q \frac{(e^{-iq} - 1) \tilde{\xi}(q, \omega)}{(L + 1) P(q, \omega)}
\]

(A.10)

where, explicitly,

\[
Q(\omega) = 1 - \sum q \frac{g(q)}{(L + 1) P(q, \omega)}
= \frac{1}{L + 1} \sum q \frac{(L + 1) (e^{i \omega} - 1) + \alpha_{\text{eff}}^\prime (1 - \bar{\rho}) (1 - e^{-iq})}{(L + 1) (e^{i \omega} - 1) + (1 - \cos k) + iv \sin k}.
\]

(A.11)

Putting (A.10) for \( \sigma \) back into (A.8) for \( \tilde{\varphi} \), we arrive at

\[
\tilde{\varphi}(k, \omega) = \frac{(e^{-ik} - 1) \tilde{\xi}(k, \omega)}{P(k, \omega)} + \frac{g(k)}{Q(\omega) P(k, \omega)} \sum q \frac{(e^{-iq} - 1) \tilde{\xi}(q, \omega)}{(L + 1) P(q, \omega)}.
\]

(A.12)

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