# APPENDIX B

In this appendix, we summarize the calculation of parameters $\omega_0$ and $\omega_1$ in equations (2) in terms of the ecological parameters *A*, *B*, and *C* (or equivalently $\mu$) in equations (1). As discussed in the main text, we assume that the parameter $\delta = 1$. The calculation involves a "reduction to normal form," which will convert equations (1) into the Hopf normal form:

$$\frac{\partial U}{\partial T} = \frac{\partial^2 U}{\partial X^2} + (\mu\Lambda_0 - \Lambda_1 R^2)U - (\Omega_0 + \mu\Omega_1 + \Omega_2 R^2)V, \qquad \text{(B1a)}$$

$$\frac{\partial V}{\partial T} = \frac{\partial^2 V}{\partial X^2} + (\Omega_0 + \mu\Omega_1 + \Omega_2 R^2)U + (\mu\Lambda_0 - \Lambda_1 R^2)V, \qquad \text{(B1b)}$$

where $R = (U^2 + V^2)^{1/2}$. This can then be converted to equations (2) by suitable rescaling.

The basic procedure for calculating a Hopf normal form is described in many books on bifurcation theory (e.g., Guckenheimer and Holmes 1983). However, typical presentations emphasize theory rather than practical implementation, and thus we think that it is helpful to summarize the practicalities of the calculation here. Much of the material in this appendix has also been presented previously in Sherratt (2001) but without some key steps required for figure 3. Extensive algebraic manipulation is required in a reduction to normal form, which is greatly facilitated by the use of a computer algebra package. A MAPLE worksheet that performs all of the calculations described below is available at http://www.ma.hw.ac.uk/~jas/supplements/lovoles/.

*Step 1: steady states and linear stability analysis*. In addition to the zero and prey-only steady states, system (1) has a coexistence steady state ($p_s$, $h_s$), where $h_s = 1/[C(A - 1)]$ and $p_s = Ah_s(1 - h_s)$. Note that $A > 1$ is required for this steady state to exist; otherwise, the death rate of the predators is too great for a predator population to be maintained. Standard linear stability analysis shows that the population represented by equations (1) becomes cyclic when the parameter *C* is above the critical value $C_{crit} = (A + 1)/(A - 1)$. The linear stability analysis also gives expressions for the complex conjugate pair of eigenvalues $\varepsilon$ of the kinetics of equations (1) at ($h_s$, $p_s$). Standard theory (e.g., Guckenheimer and Holmes 1983) implies $\Lambda_0$, $\Omega_0$, and $\Omega_1$ are given by the expansions of $\varepsilon$ up to linear terms in $\mu = C - C_{crit}$. Thus

$$\Lambda_0 = \frac{\partial}{\partial C}[Re(\mathcal{E})]\bigg|_{C=C_{crit}} = \frac{A-1}{2A(A+1)},$$

$$\Omega_0 = [Im(\mathcal{E})]\bigg|_{C=C_{crit}} = \sqrt{\frac{A-1}{A(A+1)B}},$$

$$\Omega_1 = \frac{\partial}{\partial C}[Im(\mathcal{E})]\bigg|_{C=C_{crit}} = \frac{1}{2}\sqrt{\frac{(A-1)^3}{A^3(A+1)^3B}}.$$

There is clearly an arbitrariness in the sign of $\Omega_0$ and $\Omega_1$ because there is a complex conjugate pair of eigenvalues. This choice of sign goes through to $\Omega_2$ and has no effect on model predictions; changing the sign of $\Omega_0$, $\Omega_1$, and $\Omega_2$ corresponds to interchanging *U* and *V*.

*Step 2: converting linear part to normal form.* Calculation of the coefficients $\Lambda_1$ and $\Omega_2$ is more involved. Standard theory implies that one can set $C \equiv C_{crit}$, because corrections due to changes in *C* only enter higher order terms in the normal form (Guckenheimer and Holmes 1983). Fixing *C* at this value, the next step is to do a linear change of variables so that the linear part of the equations is in normal form. For equations (1), this is achieved by setting

$$\hat{p} = \frac{p_s - p}{\sqrt{A(1-2h_s)/B}},$$

$$\hat{h} = h - h_s, \qquad \text{(B2)}$$

which gives (with $\delta = 1$) the equations

$$\frac{\partial \hat{p}}{\partial T} = \frac{\partial^2 \hat{p}}{\partial X^2} + \mu\Lambda_0 \hat{p} - (\Omega_0 + \mu\Omega_1)\hat{h} + \mathcal{F}(\hat{p}, \hat{h}), \qquad \text{(B3a)}$$

$$\frac{\partial \hat{h}}{\partial T} = \frac{\partial^2 \hat{h}}{\partial X^2} + \mu\Lambda_0 \hat{h} + (\Omega_0 + \mu\Omega_1)\hat{p} + \mathcal{G}(\hat{p}, \hat{h}). \qquad \text{(B3b)}$$

Here the functions $\mathcal{F}$ and $\mathcal{G}$ have complicated algebraic forms but are easily calculated by a computer algebra package; a simple check on the calculation is possible because both functions should be 0 with zero first derivatives at $\hat{p} = \hat{h} = 0$. Note that the signs in the change of variables in equation (B2) must be chosen to give the correct sign structure in equations (B3); this is necessary for the sign of $\Omega_1$ to be determined correctly.

*Step 3: calculating* $\Lambda_1$ *and* $\Omega_2$. Once the equations are in the form (B3), standard formulas can be used to find $\Lambda_1$ and $\Omega_2$. Methods for deriving these formulas are described in textbooks and some articles (Guckenheimer and Holmes 1983; Knobloch 1986), and here we simply repeat them:

$$\Lambda_1 = -\frac{1}{16}\left(\mathcal{F}_{\hat{p}\hat{p}\hat{p}} + \mathcal{F}_{\hat{p}\hat{h}\hat{h}} + \mathcal{G}_{\hat{p}\hat{p}\hat{h}} + \mathcal{G}_{\hat{h}\hat{h}\hat{h}}\right) + \frac{1}{16\Omega_0}\left[\mathcal{F}_{\hat{p}\hat{p}}\mathcal{G}_{\hat{p}\hat{p}} - \mathcal{F}_{\hat{h}\hat{h}}\mathcal{G}_{\hat{h}\hat{h}} - \mathcal{F}_{\hat{p}\hat{h}}\left(\mathcal{F}_{\hat{p}\hat{p}} + \mathcal{F}_{\hat{h}\hat{h}}\right) + \mathcal{G}_{\hat{p}\hat{h}}\left(\mathcal{G}_{\hat{h}\hat{h}} + \mathcal{G}_{\hat{p}\hat{p}}\right)\right],$$

$$\Omega_2 = \frac{1}{16}\left(\mathcal{G}_{\hat{p}\hat{p}\hat{p}} + \mathcal{G}_{\hat{p}\hat{h}\hat{h}} - \mathcal{F}_{\hat{p}\hat{p}\hat{h}} - \mathcal{F}_{\hat{h}\hat{h}\hat{h}}\right) + \frac{1}{48\Omega_0}$$

$$\times \left[\mathcal{F}_{\hat{p}\hat{p}}\left(\mathcal{G}_{\hat{p}\hat{h}} - \mathcal{F}_{\hat{h}\hat{h}}\right) + \mathcal{G}_{\hat{h}\hat{h}}\left(\mathcal{F}_{\hat{p}\hat{h}} - \mathcal{G}_{\hat{p}\hat{p}}\right) - 3\mathcal{F}_{\hat{h}\hat{h}}\left(\mathcal{G}_{\hat{p}\hat{h}} + \mathcal{F}_{\hat{h}\hat{h}}\right) - 3\mathcal{G}_{\hat{p}\hat{p}}\left(\mathcal{F}_{\hat{p}\hat{h}} + \mathcal{G}_{\hat{p}\hat{p}}\right) - 2\left(\mathcal{F}_{\hat{p}\hat{p}} + \mathcal{F}_{\hat{h}\hat{h}} - \mathcal{G}_{\hat{p}\hat{h}}\right)^2 - 2\left(\mathcal{G}_{\hat{p}\hat{p}} + \mathcal{G}_{\hat{h}\hat{h}} - \mathcal{F}_{\hat{p}\hat{h}}\right)^2\right].$$

Here the subscripts $\hat{p}$ and $\hat{h}$ denote partial derivatives. Thus, for example, $\mathcal{F}_{\hat{p}\hat{h}\hat{h}} \equiv \partial^3\mathcal{F}/\partial\hat{p}\,\partial\hat{h}^2$. These formulas are extremely laborious to use by hand, but a computer algebra package makes them easy to evaluate. Typically the results require considerable algebraic simplification, but this can be done automatically by computer algebra.

At this stage, it is possible to calculate the formula for the approximate amplitude of the population cycles when $\mu$ is small, which is given in the main text. The ratio of the maximum and minimum prey densities is given by

$$\frac{h_s + \sqrt{\Lambda_0 \mu/\Lambda_1}}{h_s - \sqrt{\Lambda_0 \mu/\Lambda_1}} + o(\mu^{1/2}) = 1 + \sqrt{\frac{4\mu\Lambda_0}{h_s^2 \Lambda_1}} + o(\mu^{1/2}) = 1 + \sqrt{8(A-1)\mu} + o(\mu^{1/2}).$$

*Step 4: rescaling*. The normal form equations (B1) can be converted to the required form (2) by a simple rescaling:

$$\omega_0 = \frac{\Omega_0 + \mu\Omega_1}{\mu\Lambda_0}, x = X\sqrt{\mu\Lambda_0}, u = U\sqrt{\frac{\Lambda_1}{\mu\Lambda_0}},$$

$$\omega_1 = -\frac{\Omega_2}{\Lambda_1}, t = \mu\Lambda_0 T, v = V\sqrt{\frac{\Lambda_1}{\mu\Lambda_0}}. \qquad \text{(B4)}$$

Simplification of the resulting formulas for $\omega_0$ and $\omega_1$ gives equations (3).

*Calculating* $r_{bdy}$. In figure 3, we plot the predicted variation in periodic wave amplitude as a function of $\mu$ for fixed *A* and *B*. This requires that for a given value of $\mu$, we calculate $\omega_0$ and $r_{bdy}$. The first of these is straightforward, using equations (3). For $r_{bdy}$ we require values of *u* and *v* that correspond to the predator-prey boundary values $p = h = 0$. There cannot be an exact correspondence, of course, because $p = h = 0$ is an equilibrium point in equations (1) that has no equivalent in equations (2). However, we can find an approximation to an appropriate boundary value. From equation (B2) we have that $p = h = 0$ gives $\hat{p} = p_s\{B/[A(1 - 2h_s)]\}^{1/2}$, $\hat{h} = -h_s$. The variables *U* and *V* are complex nonlinear functions of $\hat{p}$ and $\hat{h}$, but they are close to the identity when *U* and *V* are small. Therefore, because we are only attempting to derive an approximate relationship, we take $U \approx \hat{p}$ and $V \approx \hat{h}$. The final variable change, from *U* - *V* to *u* - *v*, is given by equation (B4). Thus $h = p = 0$ corresponds approximately to the point

$$u_{\text{bdy}} = p_s \sqrt{\frac{B\Lambda_1}{A\mu\Lambda_0(1-2h_s)}},$$

$$v_{\text{bdy}} = -h_s \sqrt{\frac{\Lambda_1}{\mu\Lambda_0}},$$

$$\Rightarrow r_{\text{bdy}} = \sqrt{\left\{\frac{Bp_s^2}{[A(1-2h_s)]+h_s^2}\right\}\frac{\Lambda_1}{(\mu\Lambda_0)}}.$$

## APPENDIX C

In this appendix we give more details of the calculations underpinning our predictions of periodic wave stability illustrated in figure 2. Standard theory (Kopell and Howard 1973) shows that equations of the form (2) have a family of periodic traveling wave solutions with the simple form

$$u = R\sin[(\omega_0 - \omega_1 R^2)t \pm (1-R^2)x], \qquad \text{(C1a)}$$

$$v = R\cos[(\omega_0 - \omega_1 R^2)t \pm (1-R^2)x]. \qquad \text{(C1b)}$$

Here the family is parameterized by the wave amplitude $R$, which can have any value between 0 and 1. Sherratt (2003) showed that the boundary condition $u = v = 0$ generates a particular member of this periodic traveling wave family, independent of initial conditions, with the value of $R$ given by

$$R_0 = \left[\frac{1}{2}\left(1+\sqrt{1+\frac{8}{9}\omega_1^2}\right)\right]^{-1/2}. \qquad \text{(C2)}$$

The boundary condition $u = v = 0$ corresponds to the predator-prey values $p = p_s$ and $h = h_s$. To extend equation (C2) to a realistic predator-prey context, we require

instead boundary values for $u$ and $v$ that correspond to $h = p = 0$. For general values of $\mu$, no such boundary conditions can be appropriate, because $h = p = 0$ is an equilibrium of equation (1) and has no analog in equations (2). However, in the limit as $\mu \to 0$, this is not important, because the appropriate boundary condition must be that $u$ and $v$ are infinite. This is because the values of $u$ and $v$ corresponding to a given $h$ and $p$ ($\neq h_s, p_s$) increase in proportion to $1/\mu^{1/2}$ as $\mu$ is decreased with fixed values of the other parameters. Intuitively, the system (2) corresponds to magnifying the predator-prey limit cycle when this is very small, and in this magnification process, a point significantly outside the limit cycle, such as $h = p = 0$, moves almost to infinity.

We have performed an extensive program of numerical solutions of equations (2) on a semi-infinite domain, with boundary condition $u = u_{bdy}$ and $v = v_{bdy}$. In all cases, we find that periodic traveling waves develop. However, the amplitude of the periodic waves depends on the boundary amplitude $r_{bdy} \equiv (u_{bdy}^2 + v_{bdy}^2)^{1/2}$: the circular symmetry of equations (2) means that the dependence on $u_{bdy}$ and $v_{bdy}$ must be via the combination $r_{bdy}$. Moreover, our solutions show that the wave amplitude depends on both $\omega_0$ and $\omega_1$; recall from equation (C2) that the former does not affect the wave amplitude when $u_{bdy} = v_{bdy} = 0$. In figure C1*a*, we plot the wave amplitude as a function of $r_{bdy}$, showing also the dependence on $\omega_0$.

**Figure C1:** Variation in the periodic traveling wave amplitude in the $\lambda$ - $\omega$ system (2) with $r_{bdy}$ and $\omega_0$. Here $r_{bdy}$ is the amplitude imposed by the boundary conditions on $u$ and $v$ at $x = 0$. The parameter $\omega_1 = 1.3$. In *a*, we plot wave amplitude against $r_{bdy}$ for a range of values of $\omega_0$; numerical solution results are shown by dots and joined by straight lines for ease of interpretation. In *b*, we plot (*dots*) the dependence on $\omega_0$ of $R_\infty$, the saturating value of the wave amplitude for large $r_{bdy}$. This dependence fitted very well by algebraic decay of the form $R_\infty = k_1 + k_2 \omega_0^{-k_3}$; the curve shown is given by a best fit procedure and has $k_1 = 0.8807$, $k_2 = 0.1468$, and $k_3 = 0.4914$. The results are given by numerical solution of equations (2) on a spatial domain of length 60, from $t = 0$ up to $t = 250$, with $u = v = 1/(2)^{1/2}$ imposed at $t = 0$. We use a Crank-Nicolson scheme, and numerical solutions for small $\omega_0$ are very fast. However, in order to preserve accuracy, the time step must be decreased considerably as $\omega_0$ is increased. A good test of accuracy is given by the solution with $r_{bdy} = 0$, in which case the wave amplitude is known to be 0.8801 from equation (C2). We impose the condition that the simulated amplitude is within $10^{-3}$ of this true value. For $\omega_0 = 2$, this requires only a time step of $10^{-3}$, but for $\omega_0 = 32$, we need a time step of $5 \times 10^{-6}$. The computation time thus increases considerably with $\omega_0$.

The results illustrated in figure C1*a* suggest that for given $\omega_0$ and $\omega_1$, the wave amplitude increases with $r_{bdy}$, saturating at a value $R_\infty$. Moreover, $R_\infty$ decreases as $\omega_0$ increases, and this is illustrated in more detail in figure C1*b*. The formula (3) implies that $\omega_0$ increases as $\mu$ decreases, via the dependence on $1/\mu$. Therefore, the periodic wave amplitude that will be generated in the limit as $\mu \to 0$ is the limiting value of $R_\infty$ for large $\omega_0$. Unfortunately, numerical solutions become increasingly time-consuming as $\omega_0$ increases (explained in the legend to fig. C1), so that solutions for very large $\omega_0$ are infeasible. However, results such as those in figure C1*a* suggest that the wave amplitude may become independent of $r_{bdy}$ in the limit as $\omega_0 \to \infty$. This would imply that $R_\infty \to R_0$ in this limit; recall that $R_0$ is given by equation (C2). This is confirmed by simple curve fitting of the dependence of $R_\infty$ on $\omega_0$. The curve in figure C1*b* is a best fit of algebraic decay of the form $R_\infty = k_1 + k_2 \omega_0^{-k_3}$. The fit is clearly excellent and predicts a limiting amplitude ($k_1$) of 0.8807, which is very close to the value of $R_0 = 0.8801\ldots$ (this is for $\omega_1 = 1.3$, as used in the solutions in fig. C1).

The conclusion of this work is that the wave amplitude $R_0$ given in equation (C2) does apply to predator-prey systems. This is a function of $\omega_1$, which can be converted to a function of the ecological parameters $A$ and $B$ using equation (3b). The key application of this result is that it enables prediction of wave stability. Standard theory (Kopell and Howard 1973) implies that periodic wave solutions of equations (2) are stable if and only if

$$R > \left(\frac{2 + 2\omega_1^2}{3 + 2\omega_1^2}\right)^{1/2}. \qquad \text{(C3)}$$

Substituting the formula (C2) into (C3) implies that $|\omega_1| < 1.110468\ldots$ is required for stability, and it is this condition that we have used in figure 2.

This stability condition applies only when $C$ is just above the critical value $(A + 1)/(A - 1)$; strictly, it corresponds to the limiting behavior as $\mu \to 0^+$. As $C$, and thus $\mu$, increase, $\omega_0$ and the relevant value of $r_{bdy}$ decrease. Therefore, the results discussed above and illustrated in figure C1 imply that the periodic wave amplitude increases. We can use results of the type shown in figure C1 to predict the extent of this increase in wave amplitude. For a given value of $\mu$, the formula (3a) implies a value for $\omega_0$. An appropriate value of $r_{bdy}$ can then be found by calculating the values of $u$ and $v$ corresponding approximately to $h = p = 0$. This calculation is explained at the end of appendix B; it is inevitably approximate because there can be no values of $u$ and $v$ corresponding strictly to $h = p = 0$, as explained above. However, the calculation does give a measure of how the appropriate boundary condition changes with $\mu$. The results of this study are illustrated in figure 3 in the main text.

**Figure C1:**

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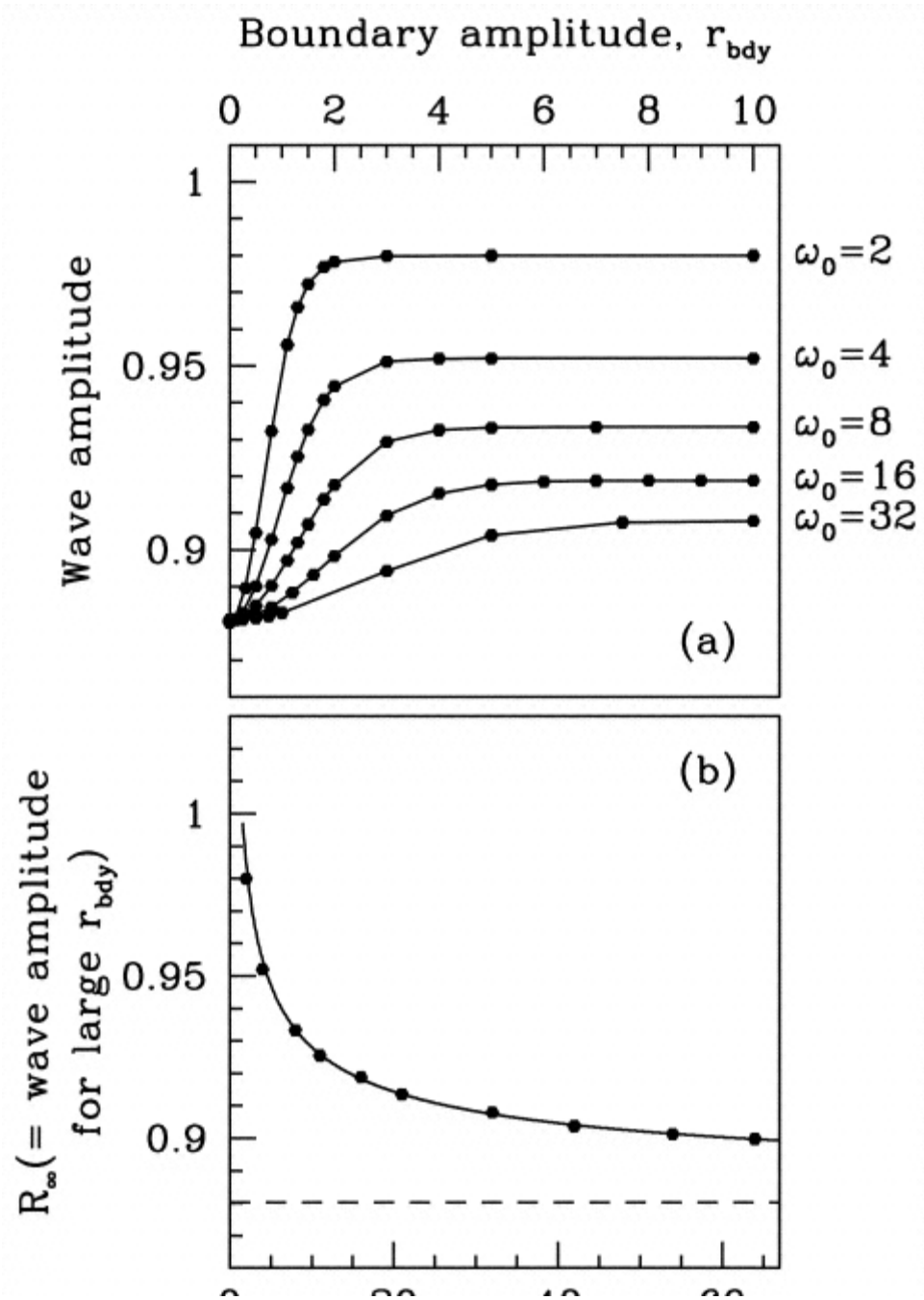
Variation in the periodic traveling wave amplitude in the $\lambda$ - $\omega$ system (2) with $r_{bdy}$ and $\omega_0$. Here $r_{bdy}$ is the amplitude imposed by the boundary conditions on $u$ and $v$ at $x = 0$. The parameter $\omega_1 = 1.3$. In *a*, we plot wave amplitude against $r_{bdy}$ for a range of values of $\omega_0$; numerical solution results are shown by dots and joined by straight lines for ease of interpretation. In *b*, we plot (*dots*) the dependence on $\omega_0$ of $R_{\infty}$, the saturating value of the wave amplitude for large $r_{bdy}$. This dependence fitted very well by algebraic decay of the form $R_{\infty} = k_1 + k_2\omega_0^{-k_3}$; the curve shown is given by a best fit procedure and has $k_1 = 0.8807$, $k_2 = 0.1468$, and $k_3 = 0.4914$. The results are given by numerical solution of equations (2) on a spatial domain of length 60, from $t = 0$ up to $t = 250$, with $u = v = 1/(2)^{1/2}$ imposed at $t = 0$. We use a Crank-Nicolson scheme, and numerical solutions for small $\omega_0$ are very fast. However, in order to preserve accuracy, the time step must be decreased considerably as $\omega_0$ is increased. A good test of accuracy is given by the solution with $r_{bdy} = 0$, in which case the wave amplitude is known to be 0.8801 from equation (C2). We impose the condition that the simulated amplitude is within $10^{-3}$ of this true value. For $\omega_0 = 2$, this requires only a time step of $10^{-3}$, but for $\omega_0 = 32$, we need a time step of $5 \times 10^{-6}$. The computation time thus increases considerably with $\omega_0$.


Boundary amplitude, $r_{bdy}$
0
2
4
6
8
10
1
0.95
0.9
Wave amplitude
$\omega_0=2$
$\omega_0=4$
$\omega_0=8$
$\omega_0=16$
$\omega_0=32$
(a)
(b)
$R_\infty$(= wave amplitude for large $r_{bdy}$)