Preface

This monograph is concerned with the mathematical analysis of patterns which are encountered in biological systems. It serves a number of purposes. First, we summarise, expand and relate the results we have obtained over the last fifteen years. Secondly, we link these results to biological applications and highlight their relevance to phenomena in nature. Thirdly, we conclude that with these studies we have initiated a systematic programme of rigorous mathematical investigation into pattern formation for large-amplitude patterns far from equilibrium in biologically relevant models. The work is organised as follows:

(i) Our goal is to consider the existence of spiky steady states in reaction-diffusion systems and select as observable patterns only those which are stable.

(ii) The investigation begins by considering a spatially homogeneous two-component activator-inhibitor system in one or two space dimensions (Chaps. 2–6).

(iii) We extend our study of these systems by adding several extra effects or by considering related systems, each motivated by their specific roles in developmental biology. This extended investigation includes the following features: the study of precursor gradients (smooth inhomogeneous coefficients) or discontinuous diffusivities; the study of finite activator diffusivity; an investigation of the effect of large reaction rates; the effect of altering the boundary conditions (from Neumann to Robin type); an investigation of the system on manifolds; the effect of adding saturation terms to the system; and replacing Gierer-Meinhardt kinetics of activator-inhibitor type by kinetics of activator-substrate type (also called Gray-Scott or Schnakenberg kinetics). In our study of reaction-diffusion systems with many components we consider the kinetics given by the hypercycle of Eigen and Schuster, introduce convection into the model, consider a system allowing for the mutual exclusion of spikes, investigate the interaction of many activators and substrates and, finally, establish exotic spiky patterns for a consumer chain model.

The existence of solutions is proved using methods from nonlinear functional analysis in either of the following settings: (i) when the linearised operator about an approximate solution is invertible in a suitable function space; or (ii) when the lin-
earised operator becomes invertible under suitable finite-dimensional projections. Case (ii) has become well-known as the Liapunov-Schmidt reduction method, and, using that approach, in a second step a finite-dimensional nonlinear problem has to be solved to establish the existence of solutions.

Concerning the stability of solutions, the approach we take allows for a rigorous analysis of the stability of large-amplitude patterned states. Large eigenvalues are investigated by nonlocal eigenvalue problems (NLEPs) which are derived by taking the limit of a rescaled eigenvalue problem and analysed using bilinear forms. While previous work introduced the NLEP approach in essentially one-dimensional settings (real line, radially symmetric, axial), we extend it to general partial differential equations without any symmetry assumptions, only requiring a certain smoothness of the boundary. The NLEP approach only provides an answer for the instabilities caused by large eigenvalues. Since there are only finitely many small eigenvalues, this reduces the stability problem to finite dimensions. Thus stability can be derived explicitly by computing the eigenvalues and eigenvectors of certain matrices.

We introduce a new approach to pattern formation in reaction-diffusion systems which differs from previous work on Turing instability (bifurcation of patterned states from unstable homogeneous steady states) [232]. These techniques also go beyond the order parameter approach reviewed in [34], which was introduced to investigate the behaviour of a system after the initial bifurcation has occurred, by including the leading nonlinear terms in the approximation, and for system parameters near the bifurcation point small-amplitude, or, more generally, slowly modulated spatially patterned states have been derived. However, both approaches are only valid for system parameters near the bifurcation point and for small-amplitude, or, more generally, slowly modulated patterns, since otherwise the nonlinear contributions or higher-order nonlinear contributions, respectively, cannot be neglected. Our approach is valid for large-amplitude patterns in the case of multiple spikes which concentrate at certain points of the underlying domain.

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