

Application of a reaction-diffusion equation to the spread of the invasive tunicate *Botrylloides violaceus*

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Introduction

Reaction-diffusion models are a type of partial differential equation (PDE) that have long been used by ecologists to analyze the migration and population dynamics of invasive species (Cosner 2008). Recent work has led to innumerable modifications on the original formulations by Fisher (1937) and Skellam (1951). Beyond the fundamental processes of growth and spread, extensions of reaction-diffusion models can be applied to age- and size-structured populations (Neubert and Caswell 2000), and incorporate environmental heterogeneity, interspecies interactions (competition, predation, mutualism, etc.), Allee effects, invasion control efforts, and long-distance dispersal. For an introduction to the use of PDEs to represent dispersal in a population ecology context, the reader is directed to Holmes et al. (1994) and the seminal papers referenced therein. For an accessible review of recent advancements in modeling invasion using reaction-diffusion equations and integro-difference equations, see Hastings et al. (2005); for a comprehensive treatment, see the textbooks by Shigesada and Kawasaki (1997) or Lewis et al. (2016).

Here, we use a simple two-dimensional reaction-diffusion model to represent the spread of the invasive ascidian *Botrylloides violaceus* in the Gulf of Maine. Colonial tunicates (or ascidians) are compound organisms formed by a mass of small zooids organized within a common gelatinous matrix. These colonies often form visible crusts on rocks, vessel hulls, and other artificial floating structures and submerged objects. Colonial tunicates also commonly grow on macroalgae and bivalves such as shellfish and oysters, making them a nuisance for the low-trophic aquaculture industry.

In New England, economic impacts from biofouling are estimated to be NUMBER. Add additional background about impact of *Botrylloides violaceus* on kelp and oyster aquaculture in the GOM here.

Most common fouling tunicate at shellfish aquaculture sites along the East coast (Carman et al., 2010)

Botrylloides violaceus has a complex life cycle, including a cyclical growth pattern dependent on both sexual and asexual reproduction. The growth and reproduction of colonial tunicates can be highly variable based on a number of environmental factors, including food availability, temperature, salinity, sediment load, and water pollution (Carver, Mallet, and Vercamaer 2006; Nelson 2014). The microscale mechanisms behind tunicate dispersion are therefore very complicated, and a fully-resolved spatiotemporal model of *B. violaceus* spread would need also to incorporate local hydrodynamic conditions, human-mediated transport, competition, and predation.

However, simple reaction-diffusion models can accurately capture population spread without relying on many assumptions and often unknown information about organism-level behavior. The value of these models is derived from their tremendous utility in ecological applications, despite abstracting many biological details (Andow et al. 1990). By eliminating unnecessary complexity and noise, simple reaction-diffusion models present a tangible method of connecting the mathematical theory of partial differential equations to observed data on invasive species, with implications for real-world ecological and economic problems.

Model Development & Theory

Here, we follow the derivation method of Lewis et al. (2016) to justify our use of the following equation to represent the rate of spread of *B. violaceus*:

$$V = \sqrt{4rD} \quad (1)$$

where $V > 0$ is the velocity (distance/time) of the advancing front of the invasive population and D and r are positive constants representing the diffusion coefficient and maximum per capita growth rate, respectively.

Since *B. violaceus* has overlapping generations and can be considered to be continuously reproducing, it is appropriate to represent the invasion dynamics using a continuous-time PDE rather than a discrete integrodifference equation. We represent the the population density of *B. violaceus* at time t and spatial coordinate x as $u(t, x)$.

Assume that the population initially occupies a finite section of the New England coastline of length L and that the initial population distribution is compact.

$$u(0, x) = \begin{cases} \phi(x) > 0 & 0 < x < L \\ 0 & \text{otherwise} \end{cases} \quad (2)$$

The reaction-diffusion model describing the population dynamics takes the form

$$\frac{\partial u}{\partial t} = D \frac{\partial u^2}{\partial x^2} + F(u) \quad (3)$$

Determining the correct form of the population growth term in (3) is challenging. Colonial ascidians generally display indeterminate growth, meaning that colony area tends to increase exponentially with time (Jackson, 1977). If we assumed simple linear population growth, our PDE would take the form

$$\frac{\partial U}{\partial t} = D \frac{\partial U^2}{\partial x^2} + rU \quad (4)$$

This is the simplest version of the general reaction-diffusion model, for a homogeneous, unstructured population growing exponentially and dispersing in a uniform, one-dimensional environment (Andow et al. 1990; Skellam 1951). However, it is unlikely that colony-scale dynamics would apply over much larger spatial scales. Leaving $F(u)$ as an unspecified function allows for the possibility of logistic growth, as in the Fisher-KPP equation:

$$\frac{\partial u}{\partial t} = D \frac{\partial u^2}{\partial x^2} + r(1 - \frac{u}{K}) \quad (5)$$

The use of nonlinear reaction diffusion models in a biological context is well-established (see Cherniha and Davydovych, 2017). However, note that for biologically reasonable choices of $F(u)$, the growth function will be bounded by the linear function, such that $F(u) \leq ru$. Thus,

$$D \frac{\partial u^2}{\partial x^2} + F(u) \leq D \frac{\partial U^2}{\partial x^2} + rU \quad (6)$$

Now, note that for compact initial conditions like (2), there exist positive constants G and σ such that we bound the initial distribution from above by a Gaussian distribution:

$$U(x, 0) = \frac{G}{\sqrt{4\pi\sigma^2}} \exp\left(-\frac{x^2}{4\sigma^2}\right) \quad (7)$$

$$\text{such that } u(0, x) \leq U(0, x) \text{ for all } x \quad (8)$$

From (6) and (8), we use the comparison theorem for PDEs to find that the solution to the linear equation in (6) provides an upper bound to the solution of the potentially nonlinear equation (3).

A detailed derivation of the solution of (4) can be found in Lewis et al. (2016). In brief, we utilize the change of variables $U(t, x) = W(t, x)e^{rt}$, reducing (4)

to the standard diffusion equation for W . We then apply Fourier and inverse Fourier transforms to the new PDE and the initial condition (7) to find that

$$W(t, x) = \frac{G}{\sqrt{4\pi(\sigma^2 + Dt)}} \exp\left(-\frac{x^2}{4(\sigma^2 + Dt)}\right)$$

Converting back to our original variable, we conclude that the solution to (4) with the initial condition (7) is a normal distribution:

$$U(t, x) = \frac{G}{\sqrt{4\pi(\sigma^2 + Dt)}} \exp\left(-\frac{x^2}{4(\sigma^2 + Dt)} + rt\right) \quad (9)$$

Now, we can quantify the spatial spread of the population by considering how quickly a level set $U(x, t) = U_c$ moves in space, where U_c could be considered a threshold of detection. In other words, below U_c it is so difficult to find the invasive organisms that for practical purposes they are not present. By rearranging (9), we can get the following expression

$$\left(\frac{x}{t}\right)^2 = 4rD + \frac{4r\sigma^2}{t} - \frac{4(\sigma^2 + Dt)}{t^2} \ln\left(\frac{U_{cr}\sqrt{4\pi(\sigma^2 + Dt)}}{G}\right)$$

As t becomes large, this formula simplifies to $\frac{|x|}{t} \rightarrow \sqrt{4rD}$. Thus, the asymptotic rate of spread is $V = \sqrt{4rD}$, as we initially sought to show.

This relationship between V, r , and D holds true for nonlinear forms of $F(u)$, can be extended to higher dimensions, and does not need to rely on the idea of a threshold of detection—in fact, true advancing fronts with asymptotic speeds given by (1) form ((Skellam 1951; Okubo and Levin 2001), Okubo and Levin, 2001). For invasion of a two-dimensional homogeneous habitat described by the reaction-diffusion equation

$$\frac{\partial u(x, y)}{\partial t} = D \left[\frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2} \right] + F(u), \quad (10)$$

the radius of the species range should increase linearly with time, with the slope of the increase given by $\sqrt{4rD}$.

This theory has been tested for numerous ecological systems and often agrees well with the empirical relationship between measured spread rates, per capita growth rates, and diffusion coefficients. Microscale observations can be used to parameterize (1) and predict the spreading rate for a given species at a geographic scale. Such spreading-speed analyses have been conducted for a number of terrestrial animal species, including the muskrat, cereal leaf beetle, small cabbage white butterfly, and grey squirrel (Andow et al. 1990; Grosholz 1996).

Spreading speed theory has also been applied to numerous aquatic species, including the brown trout, green crab, hermit crab, periwinkle, barnacle, mussels, and molluscs (MacDonald, Leroux, and Purchase 2022; Grosholz 1996; Marculis and Lui 2016; Gharouni et al. 2015). Possibly the only application of this method to a tunicate was performed by Grosholz (1996) for *B. leachi*, but his estimates of $r = 1.8$ and $D = 1800$ yielded a predicted rate of spread an order of magnitude larger than observed rates. In addition to providing insight on the spread of a specific invasive species of commercial concern, comparing the accuracy of our estimation for *B. violaceus* to the previous results for *B. leachi* could allow for broader conclusions to be drawn regarding the applicability of this approach for colonial tunicates in general.

Application

Predicting invasion speed

The diffusion coefficient, D , was calculated using the formula

$$D = \frac{2M_D(t)^2}{\pi t}$$

where $M_D(t)$ is the mean displacement of tracked organisms t time units after they begin moving (Andow et al. 1990; Skellam, 1973).

We estimated M_D using information on the dispersal potential of post-larval *Botrylloides* *sp.* colonies collected by Worcester (1994) (Table 1). *B. violaceus* can disperse naturally by rafting on eelgrass and other floating vegetation or debris (Carver, Mallet, and Vercamaer 2006; Worcester 1994). The dispersal distance/speed of rafting colonies was used rather than swimming larvae to better reflect the likely mechanisms by which *B. violaceus* has spread along the coastline. Additionally, calculating dispersal potential from larval swimming speeds would be very difficult for a species with a complex reproduction cycle in which the timing and magnitude of spawning events varies between locations and can be highly affected by environmental conditions (SOURCES).

Table 1: Calculating the diffusion coefficient

Parameter	Value
Distance traveled per colony per day (km)	0.225
Probability that a given colony will raft	0.667
Probability that a given rafting colony will reach a suitable habitat	0.5
Mean displacement (km/year)	27.38
D (km ² /year)	477.1

Eight estimates of population growth rate (r) were taken from Grey (2011), ranging from 0.87-1.89. Each r value was combined with our estimate of D to find a predicted invasion speed, V , in km/year.

Model validation

We validated our invasion speed estimates against the rate of boundary displacement for the region in which *B. violaceus* has been observed. We retrieved species occurrence data from the Global Biodiversity Information Facility (GBIF, <https://www.gbif.org/>) using the package ‘spocc’ (Owens, Barve, and Chamberlain 2024). GBIF is an international database of biological data that has been used in over 10,000 peer-reviewed scientific articles and incorporates data from a variety of sources, primarily the citizen science platform iNaturalist. Although citizen science data can contain spatial and temporal bias (Di Cecco et al. 2021), it is a valuable and widely-used tool for monitoring the spread of invasive species (Encarnação, Teodósio, and Morais 2021). Furthermore, iNaturalist observations must meet certain quality standards to be included in GBIF (<https://www.inaturalist.org/pages/help#GBIFdata>), and tunicates like *B. violaceus* have a relatively low risk of misidentification by citizen volunteers (Lawson et al. 2022).

The region of interest for the GBIF query was arbitrarily defined to be the rectangular region bounded by the coordinates (72°W, 41°N, 59°W, 50°N). We only included observations labeled as “Human Observation” in order to exclude preserved specimens located in museum collections. Although *B. violaceus* may have been introduced to the east coast of the United States as early as the 1970s (SOURCE), the earliest record in the GBIF database is from 2005.

For each year (t) since the year of the initial observation ($t_0 = 2005$), we calculated V as

$$V = \frac{\max |x_i - x_0|}{t - t_0}$$

where x_0 was the coordinate location of the 2005 observation and x_i is a single observation within the vector \mathbf{x} of locations where *B. violaceus* had been observed over the period t_0 to t . While there are various methods of quantifying macroscale patterns of species’ range expansions, similar boundary displacement approaches are common in invasion ecology (Clark, Iannone, and Fei 2018; Tobin, Liebhold, and Anderson Roberts 2007). We discarded the very low speed estimated for 2006 (1.1 km/year) as a clear outlier, but all other data was retained.

All calculations were performed in R version 4.3.2 (R Core Team 2023). R packages central to data analysis and visualization included ‘spocc’, ‘sf’, ‘leaflet’, and the tidyverse collection (Pebesma and Bivand 2023; Wickham et al. 2019; Owens, Barve, and Chamberlain 2024; Cheng et al. 2023).

Results

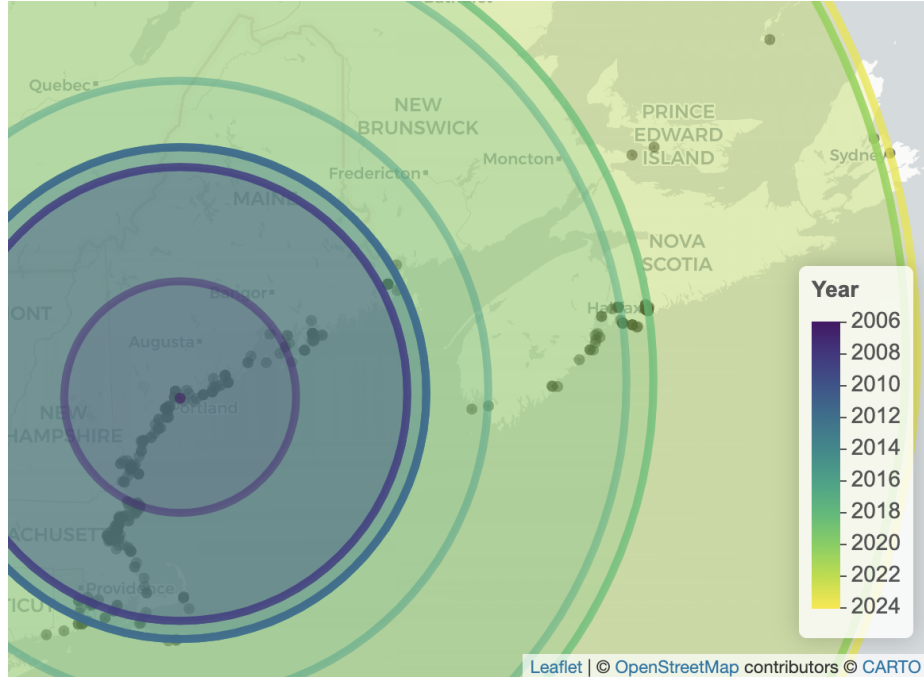


Figure 1: A map of the spread of *B. violaceus* in the Gulf of Maine. Black dots represent confirmed observations of *B. violaceus* from the GBIF database. Colored circles (centered at the location of the first observation) illustrate the expanding range.

Table 2: Summary statistics for observed and predicted *B. violaceus* invasion speed (km/year).

	Observed	Predicted
Min.	27.3	38.5
1st Qu.	32.0	42.5
Median	40.4	48.5
Mean	40.6	49.4
3rd Qu.	45.5	57.1
Max.	64.0	60.0

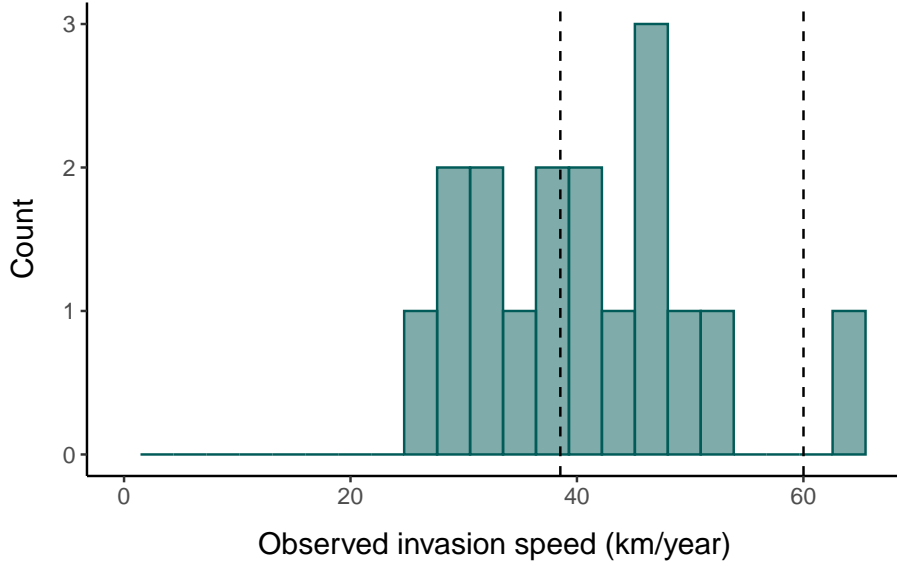


Figure 2: Histogram of observed invasion speeds for *B. violaceus* in the Gulf of Maine, calculated from GBIF species occurrence data from 2006-2024. Dashed lines represent the minimum and maximum predicted invasion speeds when varying population growth rates were used as input values.

Discussion

This model attempted to predict the macro-scale dispersal of an invasive tunicate using a simple reaction-diffusion model. Given the low biological realism of our simple diffusion model, the very strong agreement between observed and predicted invasion speeds is quite remarkable. Most studies that have applied this method of predicting invasion speed characterized their results as successful if estimates were within the same order of magnitude as observed spreading speeds. For example, Grosholz (1996) predicted the spreading speed of the tunicate *B. leachi* (a member of the same genus as to be *B. violaceus*) to be 114 km/year, which was much faster than the observed rate of 16 km/year.

In contrast, our predicted speed of 49 km/year was extremely close to the mean of 41 km/year derived from observations of *B. violaceus* made in the Gulf of Maine over the past two decades (Table 2). Both the observed and predicted invasion speeds were generally in the range of 40-60 km/year (Fig 2). While such accurate prediction is unlikely to be replicable with other data sets, it does suggest that estimating spreading speed from empirical data on local diffusion potential and experimentally-derived population growth rates could be an underutilized approach in invasion ecology.

Multiple avenues are apparent for future work modeling the spread of *B. violaceus* using diffusion-type equations. First, there exist many other possible formulations for the term representing population growth. The Fisher-KPP equation, which assumes logistic rather than exponential growth, has been well-studied from a mathematical perspective and has seen widespread application across ecological contexts (SOURCES). Other diffusion models incorporate Allee effects, an ecological phenomenon characterized by decreased individual fitness (lower per capita growth rates) at small population sizes. Accounting for Allee effects in continuous reaction-diffusion models or analogous discrete integrodifference models can alter predictions about the potential success or failure of an invasion, rates of spread, and plausible ranges of an invasive species (Keitt, Lewis, and Holt 2001; Kot, Lewis, and Driessche 1996; Liu and Kot 2019).

The model from which (1) was derived assumes a uniform environment and isotropic dispersal. In reality, invasive species are more likely to disperse into more favorable habitats, so assuming that the rate of spread does not vary based on the direction of movement is not realistic. For example, the growth and reproduction of *B. violaceus* generally increase with warmer temperatures, so in a relatively cold climate, southward dispersal may be more likely than northward dispersal.

Human-mediated introduction via hull fouling on recreational or commercial watercraft and aquaculture activities are also major pathways by which invasive tunicates are introduced to new locations (Carver, Mallet, and Vercamaer 2006). Although *B. violaceus* has a relatively low attachment strength, the small drag coefficient associated with their low profile means that its displacement velocity is above the top speeds of sailboats, barges, and other slower-moving vessels (Clarke Murray, Therriault, and Martone 2012). Clarke Murray et al. (2011) found that *B. violaceus* was attached to the hulls of 9.8% of recreational boats at nine distinct marinas in British Columbia.

Future work could utilize discrete integrodifference equations with leptokurtic dispersion kernels to account for transport via hull fouling and other potential vectors of long-distance dispersal. The potential for long-distance dispersal events via natural or human-mediated pathways often prompts the use of integrodifference equations for diffusion models of invasive populations (Lewis, Petrovskii, and Potts 2016; Lutscher 2019; Kot and Neubert 2008; Neubert and Caswell 2000). These models assume that growth and dispersal occur in distinct and asynchronous stages. The ability of *B. violaceus* to utilize multiple forms of reproduction and the fact that both larvae and post-larvae can contribute to the colonization of new habitat potentially violates the assumption of temporally separated growth and dispersion. However, stratified models that separate spatially continuous short-distance dispersal from discrete long-distance dispersal can be valuable tools to reconstruct realistic invasion dynamics (e.g., Gilioli et al. 2013) and their potential for modeling the spread of *B. violaceus* merits further investigation.

Recent work coupling deterministic models with a stochastic component has led

to major improvements in the biological realism of PDE-based invasion models. These stochastic models can account for both process and observation error, incorporating the randomness inherent in natural systems. For example, Roques et al. (2011) used a “statistical-reaction-diffusion approach” to analyze the expansion of the pine processionary moth based on moth nest presence/absence data. Using a “mechanistic-statistical” diffusion model assuming logistical growth and imperfect species observation data, Louvrier et al. (2020) were able to forecast the expanding distribution of the grey wolf in France. Applying similar methods to data on *B. violaceus* would be valuable for developing useful predictions of potential future invasions.

Finally, competition-diffusion models that represent the population growth and spread of two competing species in the same habitat admit similar traveling front solutions to those described above for the simple reaction-diffusion equation (Carrère 2018). It is often interesting to investigate the stability and long-term behavior of a system of competition-diffusion models for different parameter values, including varying the propagation speeds of the two organisms or the differential impacts of the competitive interactions on each species (Carrère 2018; Ducrot, Giletti, and Matano 2014). Experimental evidence suggests that *B. violaceus* colonies can outcompete *Botryllus schlosseri*, a different invasive tunicate that has been equally or more problematic for the New England aquaculture industry (Dijkstra, Harris, and Westerman 2007; Gittenberger and Moons 2011). However, these studies have been limited to small-scale experiments conducted on a single substrate (e.g., an oyster cage, SOURCE). Our single-species reaction diffusion model could be extended to a system of competition-diffusion equations to examine the potential impacts of competition between *B. violaceus* and *B. schlosseri* on the spread of these two species on a broader scale.

- Andow, D. A., P. M. Kareiva, Simon A. Levin, and Akira Okubo. 1990. “Spread of Invading Organisms.” *Landscape Ecology* 4 (2): 177–88. <https://doi.org/10.1007/BF00132860>.
- Carrère, Cécile. 2018. “Spreading Speeds for a Two-Species Competition-Diffusion System.” *Journal of Differential Equations* 264 (3): 2133–56. <https://doi.org/10.1016/j.jde.2017.10.017>.
- Carver, Claire E., André L. Mallet, and Benedikte Vercamaer. 2006. “Biological Synopsis of the Colonial Tunicates, *Botryllus Schlosseri* and *Botrylloides Violaceus*.” Dartmouth, NS. publications.gc.ca/pub?id=9.562383&sl=0.
- Cheng, Joe, Barret Schloerke, Bhaskar Karambelkar, and Yihui Xie. 2023. “Leaflet: Create Interactive Web Maps with the JavaScript ‘Leaflet’ Library.” <https://CRAN.R-project.org/package=leaflet>.
- Clark, Teresa L, Basil V, III Iannone, and Songlin Fei. 2018. “Metrics for Macroscale Invasion and Dispersal Patterns.” *Journal of Plant Ecology* 11 (1): 64–72. <https://doi.org/10.1093/jpe/rtw136>.
- Clarke Murray, Cathryn, Evgeny A. Pakhomov, and Thomas W. Therriault. 2011. “Recreational Boating: A Large Unregulated Vector Transporting Marine Invasive Species.” *Diversity and Distributions* 17 (6): 1161–72. <https://doi.org/10.1111/j.1472-4642.2011.00798.x>.

- Clarke Murray, Cathryn, Thomas W. Therriault, and Patrick T. Martone. 2012. "Adapted for Invasion? Comparing Attachment, Drag and Dislodgment of Native and Nonindigenous Hull Fouling Species." *Biological Invasions* 14 (8): 1651–63. <https://doi.org/10.1007/s10530-012-0178-0>.
- Cosner, C. 2008. "Reaction–Diffusion Equations and Ecological Modeling." In, edited by Avner Friedman, 77–115. Berlin, Heidelberg: Springer. https://doi.org/10.1007/978-3-540-74331-6_3.
- Di Cecco, Grace J, Vijay Barve, Michael W Belitz, Brian J Stucky, Robert P Guralnick, and Allen H Hurlbert. 2021. "Observing the Observers: How Participants Contribute Data to iNaturalist and Implications for Biodiversity Science." *BioScience* 71 (11): 1179–88. <https://doi.org/10.1093/biosci/biab093>.
- Dijkstra, Jennifer, Larry G. Harris, and Erica Westerman. 2007. "Distribution and Long-Term Temporal Patterns of Four Invasive Colonial Ascidians in the Gulf of Maine." *Journal of Experimental Marine Biology and Ecology* 342 (1): 61–68. <https://doi.org/10.1016/j.jembe.2006.10.015>.
- Ducrot, Arnaud, Thomas Giletti, and Hiroshi Matano. 2014. "Existence and Convergence to a Propagating Terrace in One-Dimensional Reaction-Diffusion Equations." *Transactions of the American Mathematical Society* 366 (10): 5541–66. <https://doi.org/10.1090/S0002-9947-2014-06105-9>.
- Encarnação, João, Maria Alexandra Teodósio, and Pedro Morais. 2021. "Citizen Science and Biological Invasions: A Review." *Frontiers in Environmental Science* 8 (January). <https://doi.org/10.3389/fenvs.2020.602980>.
- Fisher, R. A. 1937. "THE WAVE OF ADVANCE OF ADVANTAGEOUS GENES." *Annals of Eugenics* 7 (4): 355–69. <https://doi.org/10.1111/j.1469-1809.1937.tb02153.x>.
- Gharouni, A, Ma Barbeau, A Locke, L Wang, and J Watmough. 2015. "Sensitivity of Invasion Speed to Dispersal and Demography: An Application of Spreading Speed Theory to the Green Crab Invasion on the Northwest Atlantic Coast." *Marine Ecology Progress Series* 541 (December): 135–50. <https://doi.org/10.3354/meps11508>.
- Gilioli, G., S. Pasquali, S. Tramontini, and F. Riolo. 2013. "Modelling Local and Long-Distance Dispersal of Invasive Chestnut Gall Wasp in Europe." *Ecological Modelling* 263 (August): 281–90. <https://doi.org/10.1016/j.ecolmodel.2013.05.011>.
- Gittenberger, Adriaan, and Jean Moons. 2011. "Settlement and Possible Competition for Space Between the Invasive Violet Tunicate Botrylloides Violaceus and the Native Star Tunicate Botryllus Schlosseri in the Netherlands." *Aquatic Invasions* 6 (4): 435–40. <https://doi.org/10.3391/ai.2011.6.4.08>.
- Grey, Erin K. 2011. "Relative Effects of Environment and Direct Species Interactions on the Population Growth Rate of an Exotic Ascidian." *Oecologia* 166 (4): 935–47. <https://www.jstor.org/stable/41499896>.
- Grosholz, Edwin D. 1996. "Contrasting Rates of Spread for Introduced Species in Terrestrial and Marine Systems." *Ecology* 77 (6): 1680–86. <https://doi.org/10.2307/2265773>.
- Hastings, Alan, Kim Cuddington, Kendi F. Davies, Christopher J. Dugaw,

- Sarah Elmendorf, Amy Freestone, Susan Harrison, et al. 2005. "The Spatial Spread of Invasions: New Developments in Theory and Evidence." *Ecology Letters* 8 (1): 91–101. <https://doi.org/10.1111/j.1461-0248.2004.00687.x>.
- Holmes, E. E., M. A. Lewis, J. E. Banks, and R. R. Veit. 1994. "Partial Differential Equations in Ecology: Spatial Interactions and Population Dynamics." *Ecology* 75 (1): 17–29. <https://doi.org/10.2307/1939378>.
- Keitt, Timothy H., Mark A. Lewis, and Robert D. Holt. 2001. "Allee Effects, Invasion Pinning, and Species' Borders." *The American Naturalist* 157 (2): 203–16. <https://doi.org/10.1086/318633>.
- Kot, Mark, Mark A. Lewis, and P. van den Driessche. 1996. "Dispersal Data and the Spread of Invading Organisms." *Ecology* 77 (7): 2027–42. <https://doi.org/10.2307/2265698>.
- Kot, Mark, and Michael G. Neubert. 2008. "Saddle-Point Approximations, Integro-difference Equations, and Invasions." *Bulletin of Mathematical Biology* 70 (6): 1790–1826. <https://doi.org/10.1007/s11538-008-9325-2>.
- Lawson, Katherine N., Brianna M. Tracy, Maria Sharova, Jim R. Muirhead, and Alison Cawood. 2022. "Engaging Online Citizen Scientists and the Consensus Method to Monitor the Marine Biofouling Community." *Frontiers in Marine Science* 9 (April). <https://doi.org/10.3389/fmars.2022.862430>.
- Lewis, Mark A., Sergei V. Petrovskii, and Jonathan R. Potts. 2016. *The Mathematics Behind Biological Invasions*. Vol. 44. Interdisciplinary Applied Mathematics. Cham: Springer International Publishing. <https://doi.org/10.1007/978-3-319-32043-4>.
- Liu, Benjamin R., and Mark Kot. 2019. "Accelerating Invasions and the Asymptotics of Fat-Tailed Dispersal." *Journal of Theoretical Biology* 471 (June): 22–41. <https://doi.org/10.1016/j.jtbi.2019.03.016>.
- Louvrier, Julie, Julien Papaix, Christophe Duchamp, and Olivier Gimenez. 2020. "A Mechanistic–statistical Species Distribution Model to Explain and Forecast Wolf (*Canis Lupus*) Colonization in South-Eastern France." *Spatial Statistics* 36 (April): 100428. <https://doi.org/10.1016/j.spasta.2020.100428>.
- Lutscher, Frithjof. 2019. *Integro-difference Equations in Spatial Ecology*. Vol. 49. Interdisciplinary Applied Mathematics. Cham: Springer International Publishing. <https://doi.org/10.1007/978-3-030-29294-2>.
- MacDonald, Kelly J., Shawn J. Leroux, and Craig F. Purchase. 2022. "Landscape, Demographic, and Dispersal Parameters Influence the Spread and Establishment Dynamics of an Aquatic Biological Invasion." *ResearchSquare*, May. <https://doi.org/10.21203/rs.3.rs-1514165/v1>.
- Marculis, Nathan G., and Roger Lui. 2016. "Modelling the Biological Invasion of *Carcinus Maenas* (the European Green Crab)." *Journal of Biological Dynamics* 10 (1): 140–63. <https://doi.org/10.1080/17513758.2015.1115563>.
- Nelson, Jocelyn Christine. 2014. "Species invasion in the marine fouling communities of British Columbia : factors that influence invasion dynamics and how they may affect *Botryllodes violaceus*." PhD thesis. <https://doi.org/10.14288/1.0167429>.
- Neubert, Michael G., and Hal Caswell. 2000. "Demography and Dispersal: Calculation and Sensitivity Analysis of Invasion Speed for Structured Popu-

- lations.” *Ecology* 81 (6): 1613–28. [https://doi.org/10.1890/0012-9658\(2000\)081%5B1613:DADCAS%5D2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081%5B1613:DADCAS%5D2.0.CO;2).
- Okubo, Akira, and Simon A. Levin. 2001. *Diffusion and Ecological Problems: Modern Perspectives*. Springer New York. <https://doi.org/10.1007/978-1-4757-4978-6>.
- Owens, Hannah, Vijay Barve, and Scott Chamberlain. 2024. “Spocc: Interface to Species Occurrence Data Sources.” <https://CRAN.R-project.org/package=spocc>.
- Pebesma, Edzer, and Roger Bivand. 2023. “{Spatial Data Science: With Applications in r}.” <https://doi.org/10.1201/9780429459016>.
- R Core Team. 2023. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. <https://www.R-project.org/>.
- Roques, Lionel, Samuel Soubeyrand, and Jérôme Rousselet. 2011. “A Statistical-Reaction-diffusion Approach for Analyzing Expansion Processes.” *Journal of Theoretical Biology* 274 (1): 43–51. <https://doi.org/10.1016/j.jtbi.2011.01.006>.
- Shigesada, Nanako, and Kohkichi Kawasaki. 1997. *Biological Invasions: Theory and Practice*. Oxford Series in Ecology and Evolution. Oxford, New York: Oxford University Press.
- Skellam, J. G. 1951. “RANDOM DISPERSAL IN THEORETICAL POPULATIONS.” *Biometrika* 38 (1-2): 196–218. <https://doi.org/10.1093/biomet/38.1-2.196>.
- Tobin, Patrick C., Andrew M. Liebhold, and E. Anderson Roberts. 2007. “Comparison of Methods for Estimating the Spread of a Non-Indigenous Species.” *Journal of Biogeography* 34 (2): 305–12. <https://doi.org/10.1111/j.1365-2699.2006.01600.x>.
- Wickham, Hadley, Mara Averick, Jennifer Bryan, Winston Chang, Lucy D’Agostino McGowan, Romain François, Garrett Grolemond, et al. 2019. “Welcome to the {Tidyverse}” 4: 1686. <https://doi.org/10.21105/joss.01686>.
- Worcester, S. E. 1994. “Adult Rafting Versus Larval Swimming: Dispersal and Recruitment of a Botryllid Ascidian on Eelgrass.” *Marine Biology* 121 (2): 309–17. <https://doi.org/10.1007/BF00346739>.