Modelling the spread of the invasive alga *Codium fragile* driven by long-distance dispersal of buoyant propagules

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ABSTRACT

The secondary spread of an invasive species after initial establishment is a major factor in determining its distribution and impacts. Determining and understanding the factors driving this secondary spread is therefore of great importance to manage and predict invasions. In this study we constructed an individual-based model for the spread of the invasive green alga *Codium fragile* ssp. *fragile* along a straight coastline, in order to understand the factors governing spreading speed. *Codium* can spread locally through non-buoyant propagules, while long-distance dispersal depends on the wind-driven dispersal of buoyant fragments. Since fragment buoyancy is determined by light conditions, we first modelled the buoyancy of fragments, yielding a dispersal time dependent on light conditions. We then used this dispersal time, along with empirical wind speeds and directions to calculate a dispersal kernel for fragments. Finally, we incorporated this dispersal kernel into a population growth model including survival rate and fragmentation rate, to calculate a population spreading speed. We found that under current environmental conditions along the east coast of Canada, (the northernmost front of this invasion) further spread towards the northeast is possible but limited (only 4 km yr^{-1}). However, a sensitivity analysis showed that environmental shifts associated with climate change, such as more variable winds and increased disturbances that cause fragmentation, have the potential to increase spreading speed and particularly northward spread.

1. Introduction

The secondary spread of an invasive species after its initial introduction is of great importance in determining the final distribution and impact of the species (Parker et al., 1999; Molnar et al., 2008). However, secondary spread is difficult to predict as it rarely occurs at a constant speed. Rather, it involves periods of rapid spread over long distances due to movement patterns of vectors (e.g. human activity; Padilla et al., 1996) or favourable environmental conditions (McQuaid and Phillips, 2000), interspersed with long periods of little to no spread. These long-distance dispersal events ("jump dispersal") are often anthropogenically driven (Blakeslee et al., 2010), but can also occur naturally (e.g. Forrest et al., 2000; Stewart, 2006). In addition, dispersal potential and survival within a species can vary widely among individuals (or propagules) and with environmental conditions. Predicting the spread of an invasive species is thus a difficult task, but understanding which factors determine secondary spread is key to managing the impacts of invaders on ecosystems (Vander Zanden and Olden, 2008).

Mathematical models based on available data are useful tools for understanding and predicting the secondary spread of invasive species. A variety of such models have been proposed to explain species spread, beginning with reaction-diffusion models (Fisher, 1937; Skellam, 1951) and variations thereof (Hengeveld, 1989). However, these models do not take into account long-distance or jump dispersal events, which may be the most important factor in determining invasion rates (Hastings et al., 2005). More recently, individual-based models (IBMs) have been developed which can be used to calculate dispersal kernels including low probability long-distance dispersal events (Fennell et al., 2012). These models incorporate stochastic ("random") components to account for differences in the conditions experienced by individual propagules (DeAngelis and Mooij, 2005). Markov Chain Monte Carlo (MCMC)

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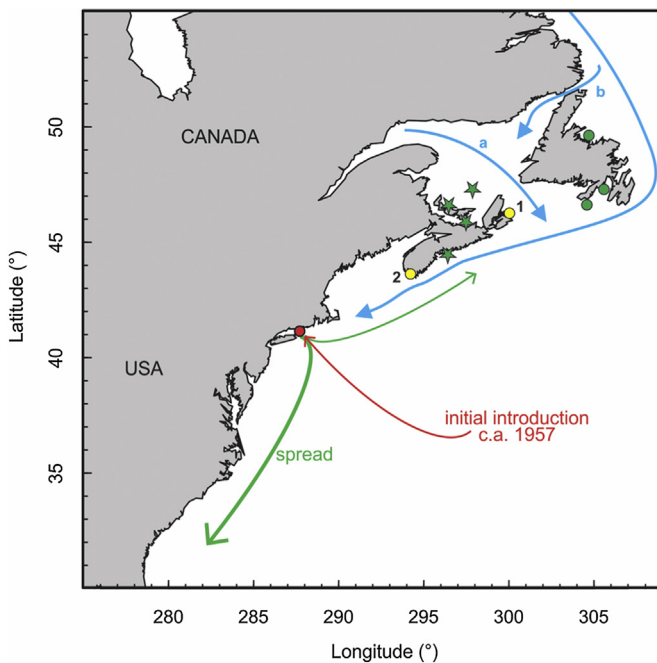
Fig. 1. Spread of *Codium fragile* in the NW Atlantic. The red line indicates the initial introduction Long Island Sound the 1950s (likely from Europe). The green arrows show the general direction of potential spread by buoyant fragments as predicted by our model, with the thickness of the lines representing the magnitude of this spread towards the southwest and northeast. The green star indicates the northernmost populations of *Codium* in eastern Canada prior to 2010, while the green circles indicate further spread to Newfoundland since 2012. Major oceanic currents are indicated in blue: (a) the Gaspé current flowing southeast through the Gulf of St. Lawrence, and (b) the Labrador current flowing around Newfoundland and down the eastern coast of North America. Points in yellow mark from where (1) weather (Sydney, Nova Scotia) and (2) wind (Baccaro Point, Nova Scotia) data used in the simulations was obtained. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

methods can be used to simulate an IBM repeatedly and obtain population-level statistics that account for variability in physical and environmental processes among individuals (Gardner and Gustafson, 2004).

In this study, we used a mechanistic IBM to estimate the dispersal kernel in an integro-difference model of population growth and spread (Lewis et al., 2006), and determine the most important factors controlling population spread along a hypothetical straight coastline. We applied the model to determine the dispersal potential and spreading speed of the invasive green alga *Codium fragile* spp. *fragile* (formerly ssp. *tomentosoides*, hereafter *Codium*) in the NW Atlantic, and compared this spread to the actual recorded spread (Fig. 1). Considered a notorious invader (Trowbridge, 1998; Molnar et al., 2008) due to its capacity for spread and impacts on benthic communities (e.g. Garbary et al., 2004; Scheibling and Gagnon, 2006), *Codium* was first recorded in eastern North America in 1957 in Long Island Sound (Bouck and Morgan, 1957), likely arriving from Europe through ballast water or aquaculture transfers (Chapman, 1999). Over 50 years, it has spread northwards to the Gulf of St. Lawrence where it has been present since approximately 1996 (Garbary et al., 1997). Spreading speed has occurred in jumps and starts (Chapman, 1999) implying a form of stratified diffusion (Shigesada et al., 1995) with long-distance dispersal events driving the invasion front (Neubert and Caswell, 2000).

Invasive *Codium* subspecies can reproduce asexually through parthenogenesis (Prince and Trowbridge, 2004) or fragmentation (Trowbridge, 1998). Fragmentation can occur spontaneously in cold waters (Fralick and Mathieson, 1972) or mechanically through natural (e.g. storms and ice scouring) and anthropogenic disturbances

(West et al., 2007). Stratified diffusion in *Codium* is thus likely due to the combined dispersal of asexually-produced propagules, and non-buoyant and buoyant fragments. Parthenogenesis and non-buoyant fragments increase local population density buoyant fragments can disperse many kilometres travelling via wind-driven surface currents before settling and forming new populations (Gagnon et al., 2011, 2015).

The use of buoyant fragments for long-distance dispersal is not unique to *Codium*; other macroalgae such as the invasive *Sargassum muticum* possess specialized air vesicles to keep them afloat (Deysher and Norton, 1982; Stewart, 2006). However, unlike many species of buoyant algae, *Codium* lacks specialized structures for buoyancy and instead relies on oxygen bubbles trapped within the thallus (Dromgoole, 1982). As these oxygen bubbles may leak out of the thallus over time, *Codium* must produce oxygen via photosynthesis to maintain positive buoyancy, providing an interesting link between sunlight and the dispersal potential of this alga (Gagnon et al., 2011).

We developed an IBM for the long-distance dispersal and inter-annual spread of *Codium* in order to determine important factors influencing spread. An estimate of the dispersal kernel of buoyant fragments was determined through independent simulations of the dispersal of many fragments. These simulations incorporated physiological processes and environmental conditions determining the period of buoyancy, as well as environmental factors affecting the dispersal distance of buoyant fragments due to wind over that period. The dispersal kernel was then used to estimate the stochastic spreading speed of *Codium* along a one-dimensional domain (Neubert et al., 2000), representing a coastline. We applied the model using environmental parameters from the east coast of Canada (the northern front of the invasion), and compared our results to the recorded spread of *Codium* in the NW Atlantic. We then performed a sensitivity analysis to determine which parameters had the greatest influence on the spreading speed of *Codium*. These parameters may be important in determining how changing environmental conditions could affect future spread and management strategies.

2. Methods

2.1. Background

The spread of invasive *Codium* was modelled in a mechanistic framework that included sub-models for sunlight and photosynthesis (Sections 2.2 and 2.3), the buoyancy of fragments (Section 2.4), dispersal times and distances (Sections 2.4 and 2.5) and population spread (Section 2.6), including stochastic components throughout (Fig. 2). For each fragment, we simulated a time series of light intensities, calculated oxygen production given those light intensities, determined the buoyancy of the fragment from the amount of oxygen it contained, and the time at which buoyancy became negative and the fragment sank. We tracked the fragment's wind-driven movement along a one-dimensional domain over the period of positive buoyancy, and the displacement upon sinking was taken to be the fragment's dispersal distance. This algorithm was repeated for 1000 fragments, which we found to be a sufficiently large number to give consistent population-level estimates of spreading speed (see Fig. A1.3). We used the distribution of dispersal distances for these 1000 fragments as an empirical estimate of the dispersal kernel in an integro-difference model of population spread.

We used environmental conditions from in late summer or early autumn in our simulations, as this is when dispersal potential is highest. At that time, fragmentation increases as adult thalli reach maximum size (Bégin and Scheibling, 2003) and rougher autumn