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A modelling approach to explore the critical environmental parameters influencing the growth and establishment of the invasive seaweed *Undaria pinnatifida* in Europe

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H I G H L I G H T S

- New individual-based model of invasive seaweed *Undaria pinnatifida*.
- Impact of light, temperature and day length on growth dynamics.
- Good quantitative agreement with field results for abundance/recruitment.
- Tool to predict future species distribution under changing climatic conditions.

A R T I C L E I N F O

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A B S T R A C T

A key factor to determine the expansion dynamics and future distribution of non-native species is their physiological response to abiotic factors and their changes over time. For this study we developed a spatially explicit, agent-based model of population growth to represent the complex population dynamics of invasive marine macroalgae with heteromorphic biphasic life cycles. The model framework represents this complex life cycle by treating the individual developmental stages (gametophytes/sporophytes) as autonomous agents with unique behaviour/growth parameters. It was parameterised to represent a well-documented invasive algal species, the Asian kelp *Undaria pinnatifida*, and validated against field results from an *in situ* population in Brittany, France, showing good quantitative agreement in terms of seasonal changes in abundance/recruitment and growth dynamics. It was then used to explore how local environmental parameters (light availability, temperature and day length) affect the population dynamics of the individual developmental stages and the overall population growth. This type of modelling approach represents a promising tool for understanding the population dynamics of macroalgae from the bottom-up in terms of the individual interactions between the independent life history stages (both microscopic and macroscopic). It can be used to trace back the behaviour of the population as a whole to the underlying physiological and environmental processes impacting each developmental stage and give insights into the roles these play in invasion success.

1. Introduction

The introduction and establishment of non-native plant and animal species can have a broad range of impacts on native species and community structure as well as economic consequences through the disruption of ecosystem services (Simberloff et al., 2013; Vilà et al., 2009). However, it is often difficult to predict the actual (and future) invasive behaviour under changing environmental conditions, since it is seldom possible to determine the source of an introduction with certainty, especially in marine environments (Rius et al., 2015). A further level of complexity comes from the fact that the response of introduced species to environmental factors may differ between the native and introduced ranges, as a consequence of trait plasticity (Davidson et al., 2011). A recent study of plant invaders pointed out an increased physiological tolerance of successful introduced species

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(Higgins and Richardson, 2014). Niche shift may thus be more common than previously assumed, which may complicate ecological-niche modelling efforts (Parravicini et al., 2015).

Seaweeds account for 20–29% of all non-native marine species in Europe and they are an important concern because of their role as primary producers in coastal ecosystems (Engelen et al., 2015; Schaffelke and Hewitt Chad, 2007; Schaffelke et al., 2006). One example of a notable invasive species on a global scale is the brown kelp *Undaria pinnatifida* (Harvey) Suringar, 1873 (Phaeophyceae: Laminariales). This has traditionally been cultivated in its native range of eastern Asia, including Japan, Korea and China (Ohno and Matsuoka, 1993; Shao-jun and Chao-yuan, 1996). However, in recent decades it has arisen as an invasive threat in Europe, North America and New Zealand among other places, due to human-mediated transport (Castric-Fey et al., 1993; Fletcher and Farrell, 1998; Floc'h et al., 1991; Grulois et al., 2011; Hay and Luckens, 1987; Silva et al., 2002; Voisin et al., 2005).

The order Laminariales (kelp) is characterised by a heteromorphic life history that consists of two distinct phases: a haploid gametophyte stage and a diploid sporophyte stage (see Fig. 1) (Bessho and Iwasa, 2010; Clayton, 1988). Each stage has specific environmental requirements for optimal growth and development, in particular with respect to water temperature, light intensity and photoperiod (daily light:dark ratio) (Floc'h et al., 1991).

One key outcome of biological invasion studies has been to point out the role played by match-mismatch between the physiological requirements of the introduced species and the local environmental conditions. It is important to define the conditions under which introduced species expand (locally or spatially) in order to predict their fate. However, in many marine species, it is difficult to make predictions due to their complex life cycle and substantial variation in physiological traits. The purpose of this study was thus to propose a modelling approach that takes into account both the individual stages of the life cycle and their specific environmental requirements, when modelling the overall population dynamics.

An agent-based (or individual-based) modelling approach was chosen in order to be able to integrate data on the basic physiological properties of *U. pinnatifida* individuals into an overall model of population growth. This allows the individual life history stages (gametophytes/sporophytes) to be represented as autonomous agents and their behaviour/interactions to be explicitly described. This so-called bottom-up approach means that the emergent dynamics, at the population level, can be traced back to the individual components (Denny and Benedetti-Cecchi, 2012; Grimm and Railsback, 2005).

The main challenge in building an agent-based model of a complex biological system such as this is the ability to parameterise it. For this reason, a thorough review of the literature was first carried out in order to gather empirical data on the basic responses of the individual life stages of *U. pinnatifida* from a mechanistic point of view. We then tested the model for accuracy and robustness by comparing it with an empirical data set from a natural population in Brittany, France (Voisin, 2007). This step was critical as phenotypic plasticity is often assumed to be an important characteristic of invasive species. Finally, we used the model to explore how some of the critical environmental parameters influence the population dynamics of the test species.

This type of low-level insight can help us to understand the role that climatic conditions play in the invasion dynamics of *U. pinnatifida* and other invasive macroalgae. The aim of this research was to develop a framework for exploring how direct and indirect effects on the life cycle and individual life history stages of macroalgae determine their population dynamics and invasive potential. This could enable better predictions about the potential future spread and range distribution of invasive seaweeds under changing climatic conditions. Furthermore, the agent-based approach means that heterogeneities in local environmental conditions, and between individual life history stages, can be explicitly accounted for in order to be able to predict the potential emergent dynamics at the population level.

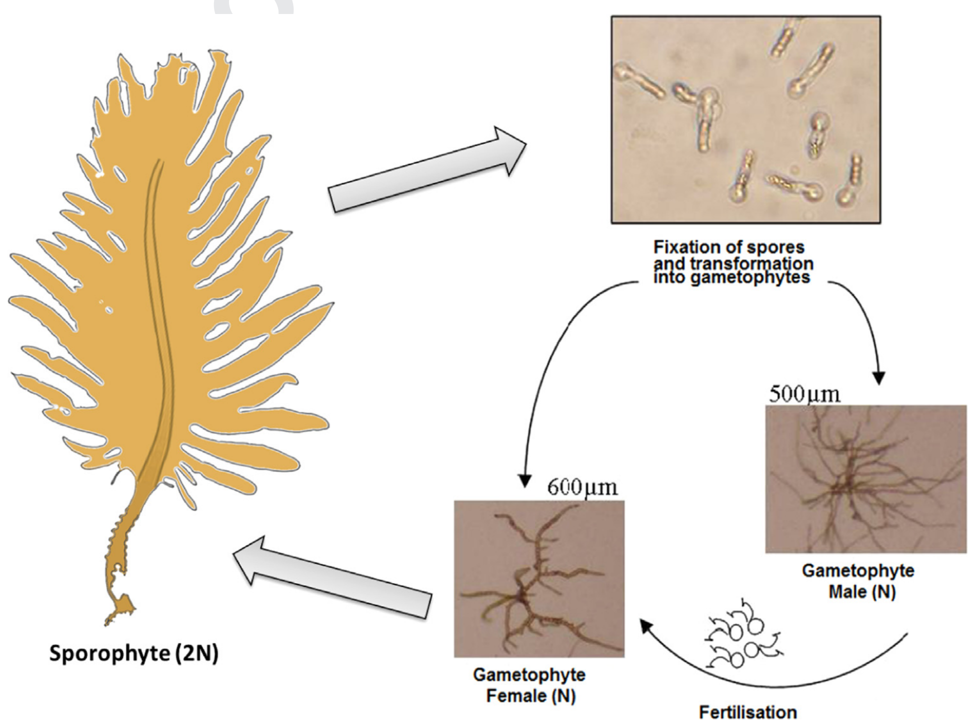

Fig. 1. Heteromorphic life cycle of *Undaria pinnatifida* consisting of microscopic haploid (N) gametophyte stages which reproduce sexually to form the diploid ($2N$) sporophyte stage (1 – 3 m in length). Photos: Daphné Grulois-Station Biologique Roscoff.