A general approach to incorporating spatial and temporal variation in individual-based models of fish populations with application to Atlantic mackerel

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ABSTRACT

Fish population dynamics are affected by multiple ecosystem drivers, such as food-web interactions, exploitation, density-dependence and the wider environment. While tactical management is still dominated by single-species models that do not explicitly account for these drivers, more holistic ecosystem models are used in strategic management. One way forward in this regard is with individual-based models (IBMs), which provide a single framework in which these drivers can be represented explicitly. We present a generic marine fish IBM that incorporates spatial and temporal variation in food availability, temperature and exploitation. Key features of the model are that it (1) includes realistic energy budgets; (2) includes the full life cycle of fish; (3) is spatially-explicit and (4) incorporates satellite remote-sensing data to represent the environmental drivers. The rates at which individuals acquire and use energy depend on local food availability and temperature. Their state variables, including life stage, size and energy reserves, are updated daily, from which population structure and dynamics emerge. To demonstrate the use of the model we calibrate it for mackerel (*Scomber scombrus*) in the North East Atlantic. Most parameters are taken from the literature, except the background early mortality rate and the strength predator density dependence, which were estimated by fitting the model to data using Approximate Bayesian Computation. The calibrated model successfully matches the available data on mackerel population dynamics and structure. We demonstrate the use of the model for management purposes by simulating the population effects of opening and closing a sector of the North Sea to mackerel fishing. Our model uses basic principles of behavioural and physiological ecology to establish how spatial and temporal variations in ecosystem drivers affect the individuals in the population. Population dynamics and structure are calculated from the collective effects on individuals. Application to a test case shows the method can fit available data well. Individual-based approaches such as this study have potential for use in strategic management because they can account for spatial structuring, food-web interactions, density dependence, and environmental drivers within a single framework.

1. Introduction

The aim of fish stock assessment is to enable management to maximise the long-term yield from a fishery, without doing irreversible damage to the stock or wider environment (Hilborn and Walters, 1992). This traditionally involved estimating one or more reference points, such as spawning stock biomass or the rate of exploitation, by fitting mathematical models to the available data on the fishery and its population dynamics (Cadrin and Dicky-Collas, 2013). Increasingly, regulatory bodies worldwide are adopting an ecosystem-based approach to

fisheries management (Garcia and Cochrane, 2005). This stems from the realisation that a stock's biological reference points will depend on other components of the ecosystem, including food-web interactions, the associated density-dependent processes (e.g. growth), and the wider environment (Skern-Mauritzen et al., 2015). Accordingly, a variety of more holistic models have been developed that can account for these drivers. Examples include age/size structured models such as OSMOSE (Shin and Cury, 2004, 2001) and LeMANS (Hall et al., 2006); food-web models such as Ecopath with Ecosim (Polovina, 1984); and multispecies oceanographic models such as Atlantis (Fulton et al., 2004). These

"ecosystem" models have been applied to strategic management questions, such as testing the response of fish populations or communities to different fishing scenarios (e.g. Kaplan et al., 2013; Thorpe et al., 2016; Travers et al., 2010).

The population effects of ecosystem drivers, including the wider environment, food-web interactions and associated density-dependent processes, often arise from their effects on the constituent individuals (Ward et al., 2016). Modelling these individual-level effects requires inclusion of processes such as adaptive traits (e.g. physiology), variation among individuals and local interactions, which traditional population models cannot easily accommodate (DeAngelis and Grimm, 2014). One way forward in this regard is with individual-based models (IBMs, also called agent-based models) (Grimm et al., 2005). In IBMs the lives of individual animals are simulated as they interact with each other and their environment (DeAngelis and Grimm, 2014). Individuals have a unique set of state variables (e.g. size and location), while the landscapes are often dynamic and characterised by environmental drivers (McLane et al., 2011; van der Vaart et al., 2016). Individual's state variables are updated when they interact with each other and their environment, and it is from simulation of all the individuals that population dynamics and structure emerge. In this way, IBMs can incorporate food-web interactions, density dependence and environmental drivers, and predict the fate of populations in defined spatially-explicit landscapes that vary over time.

IBMs have long been applied to fish populations. A major area of interest has been the merger of IBMs with bioenergetics as a way to model the response of populations to their physical and biological environment (Lett et al., 2009). Initial focus was on the food and temperature dependence of growth and survival in young-of-the-year fish (e.g. Bartsch and Coombs, 2004; Rose et al., 1999; Scheffer et al., 1995). Since then, increasing computer power has permitted the development of multi-generational bioenergetics IBMs that include the full life cycle (e.g. Politikos et al., 2015b). It is these IBMs that can address strategic management questions, including the effects of environmental drivers on migrations and reproductive output, and the effects of fishing scenarios (Lett et al., 2009). Because of their complex nature, existing full life cycle bioenergetics IBMs are typically species-specific (e.g. Pethybridge et al., 2013; Politikos et al., 2015b). Yet, there are many similarities among species in terms of their energy budgets and the way they scale with body size and temperature. The same functional forms often well describe the rates of energy uptake and its expenditure on vital processes such as maintenance, growth and reproduction (Clarke and Johnston, 1999; Peters, 1983; Sibly et al., 2013), raising the hope that a minimum generic bioenergetics model can be developed.

We present a generic marine fish IBM built on basic principles of behavioural and physiological ecology (Sibly et al., 2013; van der Vaart et al., 2016). Our model is spatially-explicit, includes a realistic energy budget and the full fish life cycle. The model landscape consists of dynamic maps of two variables derived from satellite remote-sensing (RS): sea surface temperature (SST), and chlorophyll concentration, a proxy for phytoplankton biomass, which we use to represent baseline food availability. Individuals respond to their local food availability and SST according to their energy budgets. To demonstrate the use of the model we calibrate it for the western component of the North East Atlantic mackerel (*S. scombrus*) stock. We chose this particular stock to demonstrate the potential of the IBM approach because (1) it is well-defined and subject to a specific management regime; (2) density dependence within the stock is strong, both in terms of passive competition for food (Jansen and Burns, 2015) and cannibalism (Fortier and Villeneuve, 1996); (3) its population dynamics are sensitive to environmental drivers (e.g. recruitment) (Borja et al., 2002; Villamor et al., 2011); (4) it is widely-distributed and has distinct spawning, feeding, overwintering and nursery areas (Petitgas et al., 2010), meaning spatial variation in exploitation and environmental drivers are important; (5) its wide distribution raises important management questions that cut across international jurisdictions; and (6) there is
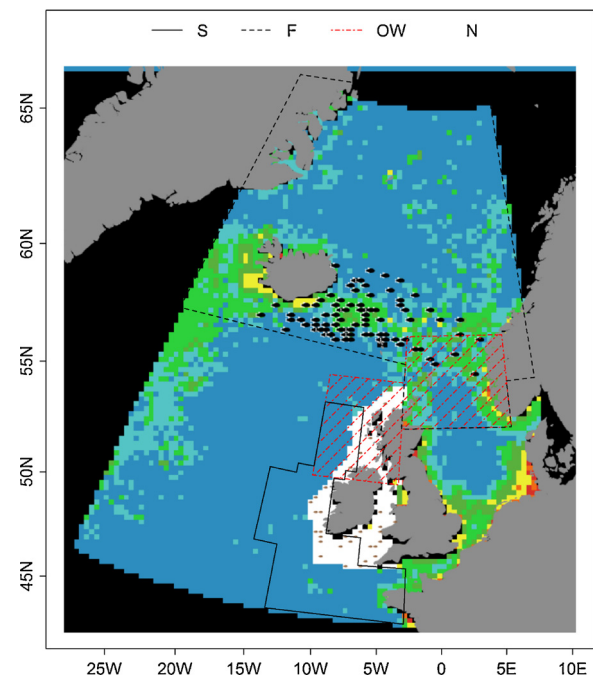

Fig. 1. An example model interface showing potential spawning S (solid line), feeding F (dashed line), overwintering OW (dotted red line) and nursery (white filled) areas (referred to later). Black fish are adults, brown fish are juveniles and the colour of the landscape corresponds to phytoplankton biomass. Phytoplankton biomass and SST are obtained from satellite remote sensing, and the landscape is updated at regular intervals. This example is taken from the case study of Atlantic mackerel described later (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

much field data available on its population dynamics and structure, and experimental data for parameterizing the energy budget. We report that the model fits data on mackerel population dynamics and structure well, and demonstrate how it may be applied by simulating the consequences of hypothetical spatial management scenarios.

2. Methodology

2.1. Model overview

In broad terms, the model landscape consists of dynamic maps of sea surface temperature SST and food availability (Fig. 1). Fish are grouped into super-individuals (hereafter termed individuals), which comprise a number of individuals with identical variables (Scheffer et al., 1995). Individuals move around the landscape according to their life cycles (e.g. to spawn or feed) (Fig. 1). Each individual has an energy budget which determines how its characteristics (e.g. body size, life stage, energy reserves) change in response to local food availability (including smaller fish) and SST. Fishing pressure at different locations determines the rate of mortality from exploitation. The abundance represented by each super-individual when it enters the model at the egg stage is determined by the amount of energy the spawning stock has put into egg production. Abundance reduces as mortality is applied throughout life. Population measures are calculated as the sum of the characteristics of all the individuals including their abundances. The model is implemented in Netlogo 5.3.1 (Wilensky, 1999).

In the following we describe the generic model and its application to Atlantic mackerel. For a full technical specification see the "TRAnsparent and Comprehensive model Evaluation" (TRACE) document (Augusiak et al., 2014; Grimm et al., 2014; Schmolke et al., 2010) in the supplementary material. In Section 2 of the TRACE we provide a model description in the standard Overview, Design Concepts