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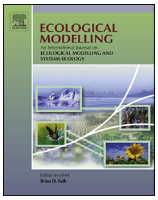

SPRAT: A spatially-explicit marine ecosystem model based on population balance equations

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ABSTRACT

To successfully manage marine fisheries using an ecosystem-based approach, long-term predictions of fish stock development considering changing environmental conditions are necessary. Such predictions can be provided by end-to-end ecosystem models, which couple existing physical and biogeochemical ocean models with newly developed spatially-explicit fish stock models. Typically, individual-based models (IBMs) and models based on advection-diffusion-reaction (ADR) equations are employed for the fish stock models. In this paper, we present a novel fish stock model called SPRAT for end-to-end ecosystem modeling based on population balance equations (PBEs) that combines the advantages of IBMs and ADR models while avoiding their main drawbacks. SPRAT accomplishes this by describing the modeled ecosystem processes from the perspective of individuals while still being based on partial differential equations.

We apply the SPRAT model to explore a well-documented regime shift observed on the eastern Scotian Shelf in the 1990s from a cod-dominated to a herring-dominated ecosystem. Model simulations are able to reconcile the observed multitrophic dynamics with documented changes in both fishing pressure and water temperature, followed by a predator–prey reversal that may have impeded recovery of depleted cod stocks.

We conclude that our model can be used to generate new hypotheses and test ideas about spatially interacting fish populations, and their joint responses to both environmental and fisheries forcing.

1. Introduction

Living marine resources and their exploitation by fisheries play an important role in sustaining global nutrition but many of the world's fish stocks are in poor condition due to overharvesting (Worm et al., 2009; Costello et al., 2016). This reduces the productivity of the stocks significantly and necessitates improved management in order to achieve a sustainable use of global fisheries resources.

Fishing, however, is not the only impact on the condition and productivity of fish stocks but long- and short-term variability of environmental parameters due to climate change or other sources of variability (such as the North Atlantic Oscillation (NAO)) imposes additional pressures (Brander, 2007). The effects of changes in the environment on fish can be direct (e.g., by altering individual growth rates) or indirect (by affecting the net primary productivity and, thus, the carrying capacity of the ecosystem). Sometimes, these factors may interact with anthropogenic influences in complex ways. For example, the expansion of oxygen minimum zones in the tropical northeast Atlantic Ocean due to climate change compresses the suitable habitat of pelagic predator fish to a narrow surface layer and, thus, increases their vulnerability to surface fishing gear (Stramma et al., 2012). The resulting high catch rates in such areas can lead to overly optimistic estimates of species abundance and, therefore, to exaggerated fishing quotas that put the affected stocks in danger of overexploitation.

Another case illustrating the complexities of how fishing and climate can interact in driven rapid ecosystem change is the recent overfishing of Atlantic cod (*Gadus morhua*) stocks in the Gulf of Maine that occurred despite stringent management practises. Here, retrospective analysis showed that this change can in large part be attributed to rapid ocean warming that has led to an unrecognized effects on recruitment and mortality, and indirectly

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rendered fisheries exploitation rates unsustainable (Pershing et al., 2015).

From such examples, it becomes apparent that fisheries management must address the effects of fishing and climate variability and change in a joined framework, accounting for the effects of different sources of mortality, including changes in natural mortality, predation, and fishing (Rose et al., 2010). Thus a more holistic ecosystem-based approach has been called for, which may focus on marine ecosystems as a whole and takes into account the interdependence of their components (Cury et al., 2008).

Ecological models that can supply this kind of information are sometimes called *end-to-end models* because they incorporate all ecosystem components from the dynamics of the abiotic environment to primary producers to top predators (Travers et al., 2007). In such models, the different elements of the ecosystem are linked together mainly through trophic interactions—i.e., by feeding (Moloney et al., 2011). Ideally, all these links between components are modeled bidirectionally (e.g., an increase in fish biomass due to feeding on zooplankton is also reflected in a decrease of zooplankton biomass). Such a two-way coupling of model elements allows to explicitly resolve at the same time both bottom-up and top-down mechanisms of ecological control. It is the combination of modeling these bidirectional links in the trophic structure and considering the dynamics of the environment that enables end-to-end models to provide long-term predictions on the development of fisheries ecosystems under environmental change. In the context of ecosystem-based fisheries management, these predictive capabilities can be used to evaluate different management scenarios with regard to their long-term effectiveness (Stock et al., 2011).

In practice, end-to-end models are typically constructed by using an existing physical and biogeochemical ocean model (for the abiotic environment as well as for nutrient and plankton dynamics) and creating a spatially-explicit fish model that can be coupled with the ocean model (Shin et al., 2010). In this context, fisheries are usually included in the model by assuming a mortality rate due to fishing (constant or changing with time), which applies homogeneously to the fish population beyond a certain lower size limit. Implementing a complete end-to-end model from scratch is discouraged by the amount of effort that is needed for developing sophisticated physical and biogeochemical models.

The most widely used fish models for end-to-end modeling are either individual-based models (IBMs), such as OSMOSE (Shin and Cury, 2001), or models based on advection–diffusion–reaction (ADR) equations, such as SEA-PODYM (Bertignac et al., 1998; Lehodey et al., 2013). IBMs offer the advantage that they are relatively easy to parametrize as their parameters are typically observable in individual fish. Additionally, these models can easily feature an emergent, dynamic food web structure. However, since—at the ocean scale—it is not feasible to simulate all individual fish of the study region, so-called *super individual* approximations of IBMs are employed (Scheffer et al., 1995). With this approach, individuals that share similar characteristics are replaced by a so-called super individual—i.e., an individual that has parameters similar to those of the individuals it represents plus an additional parameter that describes the number of individuals it stands for. This approximation technique is problematic because there is no mathematical framework for IBMs that would allow to formally study how many super-individuals are necessary to simulate the inter-individual interactions with sufficient accuracy.

Since ADR models are based on partial differential equations (PDEs), they integrate well with existing biogeochemical ocean models and feature a rigid mathematical framework with established approximation techniques for which formal error bounds can be described. Furthermore, ADR equations are derived from the principle of mass conservation and are, thus, well-suited for studying mass fluxes in marine ecosystems. However, ADR models can be difficult to parametrize because most of their parameters are usually *not* observable in individual fish and the full life cycle of the fish species is not directly represented in their main equation (only discrete age classes can be modeled).

In order to combine the advantages of IBMs and ADR models and to prevent their main drawbacks, we propose a fish model for end-to-end modeling that is based on so-called population balance equations (PBEs) (Ramkrishna, 2000). Our PBE model—which is called *SPRAT*—represents fish as density distributions on a combined continuous space-body size domain. Since PBEs are based on differential equations, they share the advantages of ADR models with regard to the integration with existing biogeochemical ocean models and to the existence of established approximation techniques. At the same time, PBE models share the distinct advantage of IBMs that most of their parameters can directly be observed in individual fish and that food web structure emerges dynamically from the model.

Potential drawbacks introduced by our PBE-based model SPRAT in comparison to IBMs and ADR models include:

1 Since we represent fish as density distributions we cannot track fish and their interactions down to the level of single individuals (as it would be possible with an IBM *not* using the super individual approximation).
2 In comparison to ADR models, the SPRAT model is associated with increased computational costs because PBE models represent the size of individuals as an additional dimension of the domain of a PDE.

For a more detailed comparison of the PBE approach with IBMs and ADR models refer to Johanson (2016, Chap. 10).

The PBE approach to fish stock modeling is similar to so-called size spectra models, which also describe fish via distribution functions on a continuous body size domain (see, e.g., Carozza et al., 2016; Andersen and Beyer, 2006; Maury and Poggiale, 2013). In the context of size spectra models, however, space is typically not resolved in the deduction of the models and is only introduced later on by assigning an instance of the respective model to each box or grid point of a discretized spatial grid (hence these models could be characterized as replicated one-dimensional or univariate PBE models). An exception to this is the APECOSM model by Maury (2010), which is designed to study apex predators (namely tuna). APECOSM is a spatially-continuous, mass-balanced size spectrum model that, like SPRAT, offers a unified continuous description of fish in both space and body size via a single distribution function. Hence, SPRAT could also be described as a spatially-continuous size spectrum model. Despite the strong similarities between these approaches, we prefer to call SPRAT a PBE model to highlight that SPRAT is derived from a model type which is widely applied in engineering and has a large body of research associated with it (especially regarding fast discretization techniques; see, e.g., Le Borne and Shahmuradyan, 2016).

In this paper, we apply SPRAT to simulate and mechanistically explore the complex interactions between the different components of the eastern Scotian Shelf ecosystem, specifically plankton and fish populations, fisheries and climate. The SPRAT model was implemented using a software engineering approach of the same name, which we presented earlier (Johanson et al., 2016; Johanson and Hasselbring, 2014a,b).