

Dynamic hybrid modelling: Switching between AB and SD designs of a predator-prey model



Gudrun Wallentin^{a,*}, Christian Neuwirth^b

^a Department of Geoinformatics – Z.GIS, University of Salzburg, Austria

^b Department of Geography, University of Munich (LMU), Munich, Germany

ARTICLE INFO

Article history:

Received 1 September 2016

Received in revised form 31 October 2016

Accepted 10 November 2016

Available online 5 December 2016

Keywords:

Hybrid model

Multi-paradigmatic modelling

Agent-based model

System-dynamics model

Predator-prey system

ABSTRACT

Entities and processes in complex systems are of diverse nature and operate at various spatial and temporal scales. Hybrid agent-based (AB) and system dynamics (SD) models have been suggested to capture the essence of these systems in a natural and computationally efficient way. However, the integration of the equation-based SD and individual-based AB models is not least challenged by considerable conceptual differences between these models. Examples of tightly integrated and dynamically switching hybrid models are rare. The aim of this paper is to expand on theoretical frameworks of hybrid agent-based and system dynamics models in ecology to support the model design process of dynamically switching hybrid models. We suggested six alternative model designs that switched between the two modelling paradigms. By the example of a fish-plankton lake ecosystem we demonstrated that a well-designed switching hybrid model can be a performant modelling approach that retains relevant spatial and attributive information. Important findings with respect to optimising computational versus predictive performance were (1) the most plausible results were produced by a spatially explicit design based on spatial plankton stocks and fish switching between individual agents and aggregate school-agents, (2) higher levels of aggregation did not necessarily result in higher computational performance, and (3) adaptive, emergence-based triggers for the paradigm switches minimised information loss and could connect hierarchical and spatial scales. In conclusion, we argue to reach beyond efficiency-oriented considerations and use emergent super-individuals as structural elements of dynamically switching hybrid models.

© 2016 Elsevier B.V. All rights reserved.

1. Introduction

Ecological systems are non-linear, complex systems with diverse processes operating at various spatial and temporal scales. Process types range from interactions between individual animals, such as catching a prey or mating, to continuous processes over spatially extended areas, such as the spread of diseases, shift of habitat ranges or scrub encroachment, and to rare events such as wildfires or floods. This diversity of natural, physical or anthropogenic processes suggests that there is no one-catches-all method to modelling. Instead, a multitude of approaches has been developed to capture the essence of different processes. Traditionally, these processes have been studied in isolation using one particular modelling method (Vincenot et al., 2011).

However, not least in the context of severe global problems, the need for synoptic views on systems has emerged to address the interplay of multiple processes in an integrated way. Two theories have been particularly influential in proposing holistic views in the study of systems: first, General Systems Theory and second, Complexity Theory (Richardson and Midgley, 2007). The two theories coincide in important aspects: A system according to both theories is more than the sum of its parts and therefore needs to be viewed and studied in a holistic way. Both theories were motivated by the quest of finding adequate ways to represent systems as integrated wholes. The system-view thus is in stark contrast to the reductionist methods of traditional approaches in science that seek to solve a problem by dissecting a system into its constituent parts with ever increasing levels of detail (Gallagher et al., 1999). Further, both theories deal with non-linear systems that exhibit surprising behaviour, which emerges from the interaction between system components. Last but not least, both theories rely on computer models to study system behaviour. The main difference refers to the conceptualisation of the structure of a sys-

* Corresponding author.

E-mail address: gudrun.wallentin@sbg.ac.at (G. Wallentin).

tem. Systems Theory conceptualises a system using a ‘top-down’ approach with a set of interconnected homogeneous aggregates that are governed by feedback loops, whereas in Complexity Theory a system emerges from ‘bottom-up’ interactions of its individual entities. Systems theory scholars have developed System Dynamics (SD) as a major method to operationalise system-theoretical models. SD is an equation-based approach that represents the exchange of matter, energy or information (‘flows’) between interconnected, aggregated system compartments (‘stocks’) over time. Complexity theorists by contrast have proposed Agent-based Modelling (ABM) as one of the most important methods to study complex, living systems. ABM is a rule-based approach that represents a system as the network of locally connected, intelligent, and often adaptive individuals (‘agents’).

Despite the common grounds of the underlying schools of thought, the respective modelling communities have stayed separate for a long time (Phelan, 1999; Scholl, 2001; Richardson and Midgley, 2007). Borshchev and Filippov (2004) conjecture that SD amongst other modelling approaches were taught to distinct groups of students resulting in separate practitioners’ communities, whereas ABM until recently has been almost purely academic. Swinerd and McNaught (2012) add the observation that also most software packages, conferences, societies and journals focus on one specific paradigm. Hamilton et al. (2015) suppose that researchers tend to favour approaches that are rooted in their own disciplines and to use familiar tools.

Nevertheless, the need to model complex and interwoven processes to address Ecological and Earth system problems has triggered interest in combined approaches. Laniak et al. (2013) pointed out that integrated environmental modelling can potentially generate new scientific insights with a reach beyond disciplinary research agendas and originate from interdisciplinary collaboration and holistic thinking. Due to pragmatic considerations and time constraints, the focus often lies on linking existing models in coupled component models rather than starting with a conceptual design of subsystems and their connecting links (Kelly et al., 2013). A problem-driven approach to adequately couple existing models over different disciplines, scales, and modelling methods is Integrated Assessment and Modelling (IAM) (Dowlatabadi, 1995; Parker et al., 2002; Hamilton et al., 2015). IAM approaches are designed as a network of model nodes that represent different subsystems and are connected through data exchange links (Kelly et al., 2013). However, insufficient understanding and representation of underlying conceptual and epistemological foundations of modelling approaches is likely to limit the usefulness and validity of integrated models (Voinov and Shugart, 2013).

In an effort to designing concepts for genuinely hybrid approaches, a number of authors have contrasted SD and AB models and discussed potentials of their integration (Schieritz and Milling, 2003; Borshchev and Filippov, 2004; Osgood, 2007; Lättilä et al., 2010; Heath et al., 2011). Based on these ideas, theoretical frameworks for hybrid modelling have been developed (Shanthikumar and Sargent, 1983; Vincenot et al., 2011; Swinerd and McNaught, 2012). Further, some tightly coupled one-platform model design frameworks have been developed to offer support for development of hybrid cross-paradigm models, for example Nova (Salter, 2013), Anylogic (Borshchev and Filippov, 2004), GAMA (Grignard et al., 2013) and Netlogo (Wilensky, 1999). Despite these advances on the conceptual as well as the technical level, hybrid AB-SD models have not yet become standard approaches. In their review on cross-paradigm simulation modelling Heath et al. (2011) use the term ‘early successes’ in terms of real-world study cases for integrated AB-SD models. Although conceptually promising, worked examples for tightly integrated hybrid approaches are rare. Thus, further exploration of tightly integrated AB-SD models in which transition and feedback between ABM and SD models constitutes

a continuous fluid process has been identified as subject to further research (Vincenot et al., 2011; Swinerd and McNaught, 2012).

In this paper we build on existing conceptual frameworks for the design of tightly integrated hybrid AB-SD models to suggest a systematic categorisation for a dynamically switching hybrid approach. The switching hybrid approach is intended to adapt the representation of system entities as the modelled system evolves and thus to dynamically optimise the trade-off between computational and predictive performance. To demonstrate our concept, we present six model designs that allow for reversible switches between the AB and SD modelling paradigms by the example of a predator-prey model with fish and plankton.

2. Frameworks for AB-SD integration

AB and SD models are complementary approaches to model systems. Many scholars argue that the choice of an appropriate modelling approach to adopt in a particular case should depend on the nature of the system at hand and the purpose of the model (Stemate et al., 2007; Swinerd and McNaught, 2012; Hamilton et al., 2015). Swinerd and McNaught (2012) suggest that many systems can be modelled in equivalent ways by both paradigms. However, they conclude that sometimes one paradigm presents a more natural choice than the other. Whereas ABMs are more powerful in representing spatial and structural realism, SD models are computationally more efficient and analytically tractable (Bobashev et al., 2007). For the domain of ecology, Vincenot et al. (2011) make a strong case that real-life systems consist of subsystems with ‘divisible entities’ such as population made of individuals as well as subsystems with ‘whole entities’ such as water in a lake. For modelling the first category, ABM is preferred, whereas SD modelling is more adequate for the latter case. Thus they conclude that hybrid models represent the structure of many complex systems in a more natural way than relying on only one paradigm. Another important difference relates to the representation of space. Whereas ABMs are usually spatially explicit, SD models deal with non-spatial or highly aggregated spatial compartments. However, intermediate, agent-oriented SD models (Akkermans, 2001; Miller et al., 2005) and spatially disaggregated derivatives of a System Dynamics model, referred to as Spatial System Dynamics models (Ahmad and Simonovic, 2004) have been developed. Vincenot et al. (2011) point out that added values and challenges of hybrid AB-SD models need yet to be fully explored. Conceptual challenges lie in integrating top-down (equation-based) with bottom-up (individual-based) models, which implies integration of spatial with non-spatial models, disaggregated with aggregated and temporally discrete with continuous models.

Several structures have been suggested to link SD and AB sub-models into an integrated hybrid model. Swinerd and McNaught (2012) present in their comprehensive literature review a framework for design concepts of hybrid AB-SD models that develops further a categorisation introduced by Shanthikumar and Sargent (1983). In this framework they suggest three types of hybrid modelling: interfaced, sequential and integrated models. In interfaced models, different system parts are modelled with independent models of different paradigms, without an exchange of information during the simulation. In sequential models, the information flow is restricted to one point in time, when the other model takes over. Integrated models, finally, are linked over the entire simulation. With ‘hybrid models’ we refer to this most tightly coupled integrated approach in this paper.

Swinerd and McNaught (2012) take a functional perspective of integrated hybrid models that comes in three manifestations: first, the SD model is within an agent (‘agents with rich internal structure’), second, a stock in a SD model bounds the behaviour of agents

(‘stocked agents’), and third, an emergent property of an ABM influences a parameter in the SD model (‘parameters with emergent behaviour’). Further, Swinerd and McNaught (2012) suggest to extend their framework by including a threshold that triggers a switch from one paradigm to the other.

A complementary categorisation to this functional view was offered in a review paper by Vincenot et al. (2011), who related to the spatial structure of AB-SD models. They distinguish four cases: (1) individuals interacting within a single SD model, (2) individuals interacting with spatially disaggregated instances of a SD model, (3) SD submodels embedded in individuals, and (4) components swapping between the SD and the AB paradigm.

Although developed independently, the two frameworks correspond well (Table 1). Subtle differences can be attributed to the viewpoints of the authors, in terms of which model governs the overall approach and finally delivers the results. Whereas Vincenot et al. (2011) seem to take a stronger ABM perspective, Swinerd and McNaught (2012) tend to conceptualise the system to be governed by the SD model. In the ‘ABM embedded in SD’ model for instance, Vincenot et al. (2011) state that the SD usually represents a dynamic system environment in which the ABM operates (an ABM-centric view that aims at system understanding, see also Lorenz and Jost 2006) or in special cases computes SD parameters dynamically (the SD-centric perspective that aims at problem solving). The latter view matches with Swinerd and McNaught (2012) concept of ‘SD parameters with emergent behaviour’. Both frameworks conclusively suggest further research to be directed towards the development of a switching approach termed ‘swapping models’ in Vincenot et al. (2011) and ‘switching concepts’ in Swinerd and McNaught (2012) to jump back and forth between the paradigms. In the following we elaborate alternative designs for switching models as a means of connecting multiple hybrid structures into one single model, which is expected to offer greater flexibility in the representation of complex systems.

3. Switching hybrid approach

Following from the previous chapter, we can distinguish between four *representations* of system entities: agents, stocks, super-agents (stocks embedded in agents), and spatial stocks (stock embedded in cells of a cellular automaton). In a static hybrid model, different representations can be combined into a model *configuration*, where for example one entity is represented by agents and another entity by spatial stocks. A *design* of a dynamic hybrid model can reversibly switch between two alternative configurations. Further switches into alternative configurations could add to it. However, additional switches do not conceptually differ from a one-switch system and are not discussed further here.

A simple system with two populations – e.g. a predator-prey system – can thus be configured in 16 alternative ways ($4 * 4$ representations). Theoretically, it is possible to define $120 (15 + 14 + \dots + 1)$ alternative designs that switch between these configurations. However, some designs are more meaningful than others. To identify the most relevant designs of a dynamic hybrid model, we start from two assumptions. First, we assume that a hybrid AB-SD model represents at least one entity by individual agents at some point during the simulation, usually at the simulation start. Second, we assume that a population of smaller individuals with smaller home ranges and higher abundance are equally or more abstracted than a population of large individuals.

Based on these two assumptions, Table 2 shows a matrix of reasonable configurations (circles) and model designs that can reversibly switch between these configurations (arrows) for a hybrid model of a predator-prey system. In all cases, the predator population is represented by individual agents at the simulation

start. Depending on the size of animals in the prey population, two main cases can be distinguished. If prey are of about the same scale level, the prey are initially represented by agents or super-agents (blue circles in Table 2). This structure is typical for an AB model configuration that switches to a hybrid configuration during simulation. In this case, the smaller sized prey switch into a representation of increased level of abstraction (blue arrows in Table 2). However, if the size of prey animals is smaller by an order of magnitude compared to their predators, it is more adequate to represent the abundance of prey by an equation-based approach as stocks or spatial stocks (black circles in Table 2). In this genuinely hybrid AB-SD configuration, the predator population is the main target of abstraction during simulation (black arrows in Table 2). For a predator-prey model with one reversible switch, there are thus twelve alternative model designs.

4. Case study: plankton – fish model

A model of a fish-plankton ecosystem was developed to demonstrate alternative designs of a switching AB-SD model. As plankton is an order of magnitude smaller than fish, this system was represented with agents for the fish population and a stock or spatial stocks for the plankton. Hence, the two initial model configurations were first, fish agents with a plankton stock and second, fish agents with spatially disaggregated plankton stocks. These two initial configurations could switch into five further configurations of higher aggregation. Thus, there were six model designs based on seven alternative model configurations. For each of the six designs a model was implemented to demonstrate the alternative realisations of the switching approach for the hybrid fish-plankton model.

The presented designs all ascribed to the same conceptual fish-plankton model. Agent rules and parameters as well as flow equations and change rates corresponded with each other as much as possible. The different model designs were not calibrated individually. The model designs were implemented in the NetLogo modelling software (Wilensky, 1999). The source code of the presented model designs are available for download at the OpenABM model library: <https://www.openabm.org/model/5254>.

4.1. Purpose

The fish-plankton model represented the dynamics of a fish population in a lake in response to plankton abundance. The purpose of the model was to represent spatio-temporal population dynamics of plankton-feeding fish. The model specifically aimed to capture the dynamics of a small fish population that is governed by stochastic events of local interactions as well as the dynamics of a large population that is limited by the abundance of plankton biomass for feeding. For its specification the model partly borrowed from literature on Alpine whitefish (*Coregonus laveretus*) in the lake Attersee in Austria, complemented with fictitious parameter values (Table 4).

4.2. Entities, state variables and scales

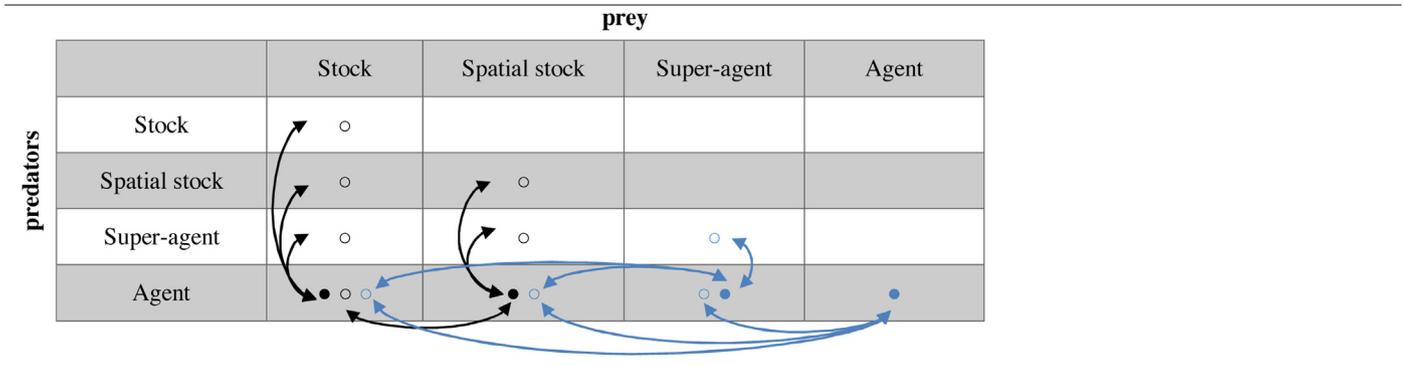
The entities in the model were fish and plankton. Depending on the design, fish were represented as agents, school-agents, spatial stocks or stocks. The plankton was represented either by a stock of a SD model or by spatial stocks in a cellular automaton. State variables were the number of fish and the amount of plankton biomass in tons.

The temporal scale of the model had a resolution of one day and extended over a simulation period of one century. The lake was roughly rectangular with dimensions of about 20 km by 2 km amounting to 46 km² surface area in total. In spatial variants of the model, the plankton was distributed over a cellular automaton grid

Table 1
Structures of integrated AB-SD models proposed in the literature. The frameworks suggested by Vincenot et al. (2011) and the integrated design concepts described by Swinerd and McNaught (2012) can be summarised into four classes.

		Vincenot et al. (2011)	Swinerd and McNaught (2012)
ABM embedded in SD		individuals interacting within a single SD model	stocked agents OR parameters with emergent behaviour
ABM embedded in Spatial SD-stocks		individuals interacting locally with multiple spatial SD models	Same as above, but “there is no spatial component in any of the [published] examples”
SD embedded in ABM (‘super-agent’)		SD submodels embedded in individuals	agents with a rich internal structure
Switching AB-SD		components swapping between the SD and the AB paradigm	switching concept

Table 2
Designs of a dynamically switching hybrid predator–prey model. Circles show reasonable configurations of how system entities are represented in the model. Filled circles represent starting configurations and unfilled circles represent configurations after the switch. Arrows show the alternative designs that reversibly switch between model configurations. Black representations and designs refer to systems in which predators are of an order of magnitude larger than prey, blue ones refer to systems in which predators and prey operate at roughly the same spatial scale.



with a cell size of 200 m by 200m. Fish movement was represented in continuous vector space.

4.3. Process overview and scheduling

A single fish agent moved straight ahead until it sensed other fish, to which it adapted its movements according to the three rules of the boids model (Reynolds, 1987). From this behaviour fish schools emerged and grew over time. School membership was a prerequisite to successful reproduction in the ABM. Under optimal conditions, an annual offspring of five fish per mature female survived the first year. Female fish laid the eggs close to the shoreline out of which young fish developed independently from any fish school. The fish matured at the age of four and reached a maximum age of six years, but may have died of starvation earlier. A fish agent consumed 2.7 g plankton per day under maximum plankton availability. Lower plankton availability controlled the energy budgets of fish in the order of maintenance, growth and reproduction (Sibly et al., 2013); see Table 3 for details.

Plankton biomass exhibited a logistic growth. The carrying capacity of plankton in the lake was assumed to be 2300 tons. In spatial variants of the model, plankton diffused 10% of its biomass per month into neighbouring cells.

The fish population was initialised with 25 individual fish agents, which is a situation close to extinction. Fish age and sex were attributed randomly from a uniform distribution. The individual locations in the lake were also assigned randomly. Plankton was set to 2150 tons, which is a value close to the carrying capacity of the lake.

As the fish population grew to a viable population size that had organised itself into schools of fish, a trigger caused the agents to switch to a more aggregate representation: school-agents, spatial stocks or stocks. If the fish population fell below 50 fish, the model switched back to its initial configuration (see Section 4.4 for a more detailed description of switches).

4.3.1. Configuration 1: Agent (fish) – Spatial stock (plankton)

Configuration 1 was the most disaggregate configuration alternative for the fish–plankton model. Together with Configuration 2 it was one of the two starting configurations of the proposed model designs. Its structure was a fish ABM embedded in a spatial raster grid of plankton SD stocks (Fig. 1). Fish agents flocked and thus they organised themselves into schools over time. The flocking behaviour was based on the flocking model in the NetLogo model library (Wilensky, 1998).

Plankton abundance and diffusion was modelled by means of a cellular automaton. Each of the cells represented independent one-stock SD model clones, where the stocks held the respective values for the local plankton biomass. Plankton biomass stocks grew logis-

Table 3
Plankton availability controlled fish agents according to their individual energy budgets.

Energy budget	Equations to calculate energy states for an agent
Energy _{ingested} (E_i)	$E_i = 2.7 * \frac{\text{planktondensity}}{\text{planktondensity}+2}$
Energy _{maintenance} (E_m)	$E_m = 0.005 * (\text{age} * 100)^{0.75}$
Energy _{growth} (E_g)	$E_g = 0.5 * (\text{max}E_i - E_m)$
Energy _{reproduction} (E_r)	$E_r(t + 1) = E_r(t) + E_i(t) - E_m(t) - E_g(t)$

Table 4

Model parameters are stated together with an assignment to the relevant model design types (asterisks). Literature sources are given, where applicable.

Model parameter	value	agent	School-agent	Spatial stock	Stock	Source
Lake size	46.5 km ²	*	*	*	*	Hofbauer (2009)
Simulation period	100 years	*	*	*	*	–
ABM step increment	1 day	*	*	*	*	–
CA grid size	200 m	*	*	*	*	–
Maximum age of fish	6 years	*	*	*	*	Ecker (2003)
Age of fish maturity	4 years	*	*	*	*	Froese and Pauly (2016)
Max. offspring per female, mature fish	5 fish	*	*	*	*	Brown et al., (1991); Kuparinen et al. (2014)
Fish feed per day	2.7 g	*	*	*	*	Einsele (1942); Tolonen (1998)
Speed of fish and fish schools	20 m per day	*	*	*	*	Assumed
Min. number of fish in school	50 fish	*	*	*	*	Assumed
Max. number of fish in school	5000 fish	*	*	*	*	Assumed
Max. turn towards plankton-rich cells	15°	*	*	*	*	Assumed
Max. turn to avoid other schools	25°	*	*	*	*	Assumed
Plankton diffusion rate	10% per month	*	*	*	*	Assumed
Carrying capacity of plankton in the lake	2300 tons	*	*	*	*	Schaber (1985)
Plankton growth rate	0.01	*	*	*	*	Kissman et al. (2013)
Fish growth rate	0.002	*	*	*	*	Derived from ABM parameters
Initial plankton biomass/lake	2150 tons	*	*	*	*	–
Initial number of fish	25 fish	*	*	*	*	–
Initial fish age	Random, 0–6 years	*	*	*	*	–
Initial fish sex	Random, 50% chance	*	*	*	*	–

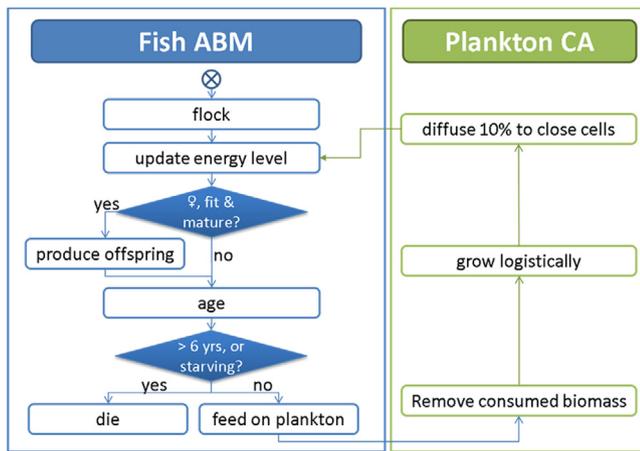


Fig. 1. The process flowchart of Configuration 1, which is the most disaggregated configuration of the fish-plankton model: it represents fish as individual agents and plankton as spatial stocks in a cellular automaton.

tically limited by the carrying capacity of a lake cell. Each time step, the amount of consumed plankton was subtracted from the local plankton biomass. The spatial connection between adjacent plankton stocks was governed by the cellular automaton (CA), which diffused ten percent of its stock to its eight neighbouring cells per day.

4.3.2. Configuration 2: Agent (fish) – Stock (plankton)

Configuration 2 was the second alternative for an initial model configuration in this case study. Its structure is similar to Configuration 1, except for the representation of plankton in a non-spatial aggregate stock. Due to the non-spatial representation of plankton, fish were not restricted by local food shortages and they did not direct their movements towards plankton.

4.3.3. Configuration 3: School-agent (fish) – Spatial stock (plankton)

In this configuration, a school-agent represented a group of schooling fish through a single school-agent with an embedded stock that governed the population dynamics. School-agents swam towards the most plankton rich cells in their Moore neighbourhood, but at the same time they avoided other schools. Growth of a fish population in a school-agent was limited by plankton resources

Table 5

Flow equations of SD processes.

SD process	Flow equation
Fish growth	$r\text{-fish} * \text{fish} * (\text{plankton}/K\text{-plankton})$
Fish mortality	$\text{fish} * (1 - ((\text{plankton}/K\text{-plankton}) \hat{0}.015))$
Plankton growth	$\text{plankton} * r\text{-plankton} * (1 - \text{plankton}/K\text{-plankton})$
Plankton decay	$\text{fish} * 0.0000027$

according to the flow equations in Table 5. As fish reached maturity at the age of four, there was a four-year delay in the feedback from the fish stock to fish growth (Fig. 2). As NetLogo does not support delayed feedback in its built-in System Dynamics Modeler, the delay was implemented by means of conveyor stocks. In contrast to the commonly used reservoir stocks, conveyor stocks store the population size increment for each time step in an array. The sum of the increments in the array equals the total amount of fish in the school stock. For each school, two coupled conveyor stocks were used to represent the fish population: one for juvenile fish and one for mature fish. The population in both fish stocks could decline due to starvation, but only the amount of fish in the mature fish stock enters in the growth equation of the fish population. Natural death of old fish was implemented by deletion of the last value in the conveyor stock each daily time step.

4.3.4. Configuration 4: School-agent (fish) – stock (plankton)

The structure of Configuration 4 is analogous to Configuration 3 except for the aggregated representation of plankton.

4.3.5. Configuration 5: Spatial stock (fish) – Spatial stock (plankton)

In this configuration, fish were no longer represented in an agent-based paradigm, but by an equation-based approach. It was configured as a SD model with two spatially discretised stocks that interacted locally. In contrast to the previous configurations, there was no explicit possibility to implement fish movement. Instead, spatial redistribution could be represented by diffusion. However, diffusion would be a completely different kind of process compared to active movement. Further, computation of diffusion between spatially disaggregated conveyor stocks would demand high computational power for the array calculations. For reasons of simplicity, this configuration therefore assumed that schooling fish were territorial and stationary. Fish populations were not re-

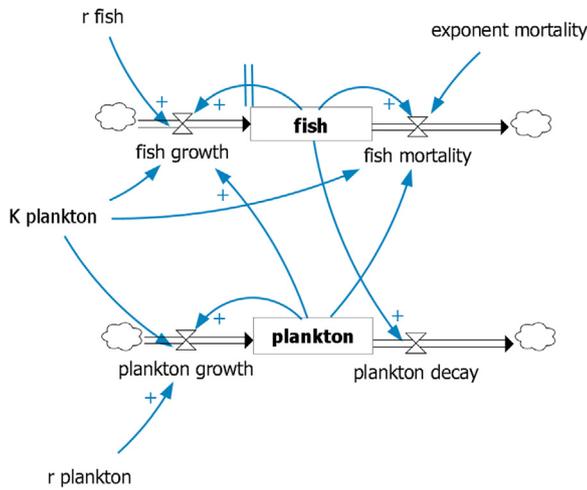


Fig. 2. The stock and flow diagram of Configuration 7, which was a pure SD model.

Table 6

Each design switches between two distinct configurations, so that one of the two populations toggles between a lower or a higher degree of aggregation.

Design	Configurations	Switch
Design 1	Conf. 1 ↔ Conf. 4	Fish: agent ↔ school-agent
Design 2	Conf. 1 ↔ Conf. 6	Fish: agent ↔ spatial stock
Design 3	Conf. 1 ↔ Conf. 7	Fish: agent ↔ stock
Design 4	Conf. 2 ↔ Conf. 3	Fish: agent ↔ school-agent
Design 5	Conf. 2 ↔ Conf. 5	Fish: agent ↔ spatial stock
Design 6	Conf. 2 ↔ Conf. 1	Plankton: spatial stock ↔ stock

cated between cells, whereas plankton diffused between cells as in the previous configurations.

4.3.6. Configuration 6: Spatial stock (fish) – Stock (plankton)

Configuration 6 was structured in analogy to the previous configuration, but with an aggregated plankton stock. The spatial distribution of fish populations in the lake was spatially explicit, but their interaction with plankton was global due to the aggregated plankton stock.

4.3.7. Configuration 7: Stock (fish) – Stock (plankton)

This most aggregated configuration was a conventional SD model with two coupled stocks. Fig. 2 shows its structure in a stock and flow diagram. Table 5 summarises the respective flow equations. In this configuration, plankton grew logistically until it reached its carrying capacity. Plankton decay related positively with the fish population. Fish growth was coupled with relative plankton abundance and with the fish stock by a delay of four years. Fish mortality was coupled with the relative abundance of plankton: the less plankton biomass was available, the more fish starved.

4.4. Model designs and switches

Six designs of dynamically switching fish-plankton models were implemented based on the configurations described above (Table 6).

In Designs 1 to 5, the switch of individual fish agents into a more aggregated representation was triggered by the emergence of fish schools. The point of time, when schools emerged was defined differently in the designs. For the switch from agents to a stock or spatial stocks, school emergence was the time, when all mature fish belonged to a school. In this case, the entire model switched into another configuration. For the switch from agents to a school-agent the automatic detection of an emergent school was operational-

ized by using a simple threshold of 50 fish. This implementation allowed for gradual transitions. A school of individual fish may have switched into a SD embedded in a school-agent, while single fish and smaller schools still remained in ABM mode. The school-agent replaced the schooling fish at their centre point. Each school could hold a maximum of 5000 fish. Surplus fish in the school-stock were converted into individual fish-agents that were expelled from the school. Fish-agents in the vicinity of schools-agents joined the school stock, whereas fish-agents in the vicinity of other fish-agents flocked until a new school eventually emerged.

The reversed switch back from aggregated model configurations to the initial configuration was invoked as soon as the total fish population fell below a switch threshold of 50 fish. The spatial distribution of the fish populations at the time of the switch was preserved by a stochastic selection of the remaining fish after fishing from existing schools. For the plankton initial SD structures were restored. The fish ABM was parameterised analogously to the initialisation phase of the model.

In Design 6, the switch related to the state of plankton. As soon as the spatial heterogeneity of plankton was negligible, the switch from spatial stocks to a stock was triggered. The trigger was operationalised as the point in time, when the standard deviation of plankton biomass per cell fell below 0.5 percent. The reversed switch was invoked, when the amount of consumed plankton per day exceeded a threshold of 1 kg per day and thus may have had the potential to impact the spatial plankton distribution. These low thresholds were chosen to be able to demonstrate the switching effects for low population numbers.

4.5. Analysis of simulation results

The comparison between alternative model designs was based on the dynamics of the fish and plankton populations, their spatial arrangement and the respective processing time. Two simulation experiments were conducted. First, the long-term population dynamics was assessed in a 100-year simulation experiment. Second, the impact of switching forth and back between model configurations was assessed in a simulation experiment with repeated fishing events. In this fishing experiment the population was reduced to the initial number of 25 fish, once the fish population exceeded 500 fish.

For both simulation experiments, the number of fish, the amount of plankton biomass and the elapsed time was recorded at each time step. All models were simulated on one core of a standard desktop computer (CPU = 2.83 GHz and 8 GB RAM). At the end of each simulation, the spatial distribution of fish and plankton was exported.

5. Results

5.1. Population dynamics in the 100-year simulation

In all designs, the population dynamics exhibited the expected logistic growth dynamics. The fish population grew only slowly in the beginning, and then accelerated until the amount of plankton limited further growth and the fish population levelled in at an equilibrium. The plankton biomass reacted accordingly until both populations reached a stable state (Fig. 3). However, the population numbers differed considerably between the designs (Table 7). Fig. 4 shows the spatial distribution of plankton and the corresponding location of fish and schools of fish.

Design 2 (Agent/stock – spatial stock/stock) and Design 3 (Agent/stock – stock/stock) resulted in the largest fish population numbers with about 765,000 fish. These two designs exhibited almost equal growth dynamic plots for the 100-year simulation.

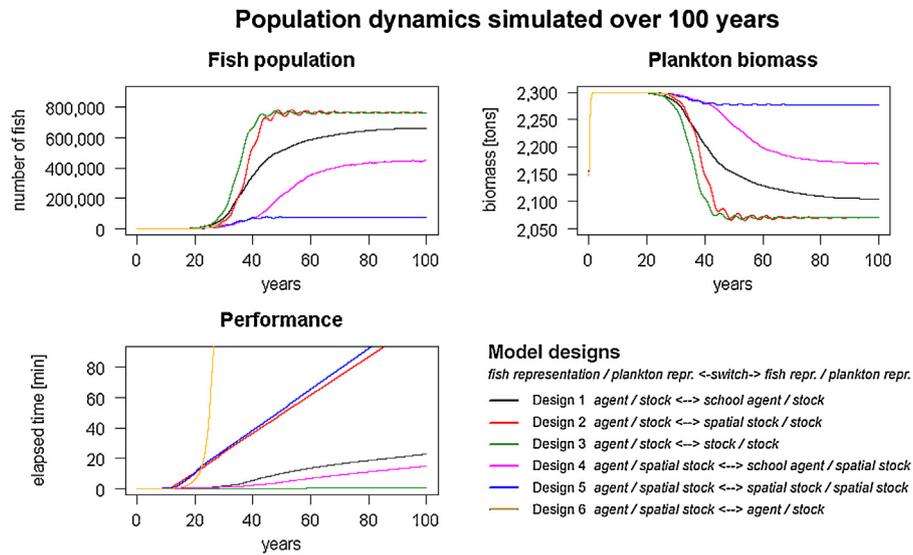


Fig. 3. Comparison of fish population dynamics (top left), plankton biomass (top right), and simulation performance (bottom left) for the six designs.

Table 7
Population sizes and elapsed time after 100 simulated years.

Switching hybrid model	Fish [number]	Plankton [tons]	Elapsed time [min]
1 Agent/stock – school-agent/stock	660466	2105	23.0
2 Agent/stock – spatial stock/stock	764130	2071	112.1
3 Agent/stock – stock/stock	765046	2071	0.51
4 Agent/spatial stock – school-agent/spatial stock	453872	2168	15.0
5 Agent/spatial stock – spatial stock/spatial stock	75641	2277	118.3
6 Agent/spatial stock – agent/stock	–	–	>700

In their aggregated configurations after the switch, both designs had the structure of a non-spatial two-stock SD model. The spatial stocks in Design 2 had no effect, as all interactions with the plankton stock were global. Population growth curves showed the typical damped oscillations of an equation-based model. In terms of processing time, Design 3 clearly outperformed all other models with an elapsed time of only 31 s, whereas Design 2 finished the 100-year simulation after 1 h 52 min.

Design 1 (Agent/stock – school-agent/stock) was also not restricted by the abundance of local resources, but nevertheless the growth was limited due to spatial self-organisation of fish. As schools were restricted with a maximum number of 5000 fish and the formation of new schools needs some space, population growth

was eventually restricted by the available spatial resources. Due to this effect, the final population size is by more than 100,000 fish smaller than in the Designs 2 and 3.

Design 4 (Agent/spatial stock – school-agent/spatial stock) is additionally restricted by the local availability of plankton resources, which diminishes the final population size by another 200,000 fish to the most plausible simulation result of approximately 450,000 fish.

In Design 5 (Agent/spatial stock – spatial stock/spatial stock) plankton and fish were both represented as spatial stocks. In contrast to the plankton, fish populations stayed stationary in their cells, as they were populated at the time of the switch. Resource

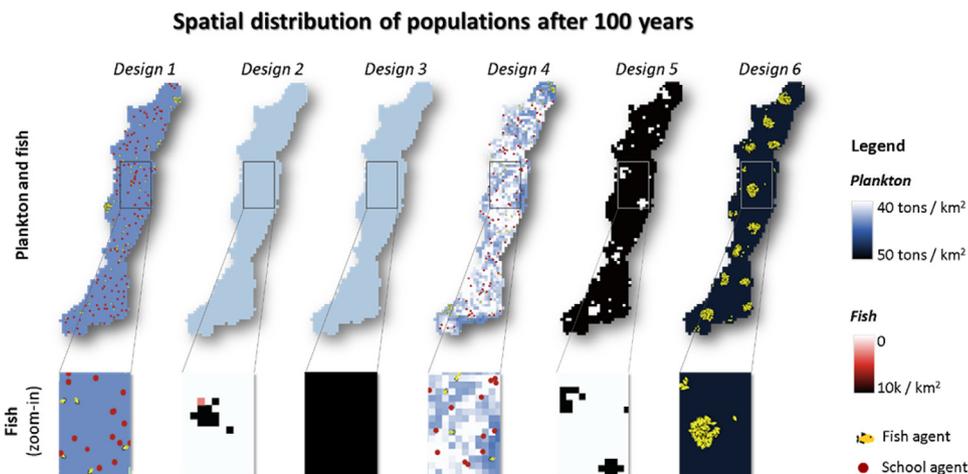


Fig. 4. Final state of the simulation environment after 100 simulated years for Designs 1 to 5, and after 30 years for Design 6, respectively.

limitations thus came into place early and fish numbers only reached a maximum level of about 75,000 animals.

Design 6 (Agent/spatial stock – agent/stock) crashed after 11 h 42 min at 30 simulated years and a population of 30,000 fish, because the maximum allocated memory (java heap size) of 5 GB was exceeded. A switch of predator agents to more aggregate representations is thus necessary to successfully simulating the presented design on a desktop computer.

5.2. Switching effects

The effects of multiple switches between the alternative configurations can be seen in Fig. 5. Fishing events were induced six to eight times within 100 years. The fish population dynamics of the disaggregated (black) design was continued by the aggregated (brown) design until the total number of fish exceeded the threshold of 500 fish, at which fishing reduced the number of fish and thus triggered the reversed switch. As the switch to aggregated configurations depended on the stochastic emergence of fish schools, the point in time when the switch was triggered varied. In Designs 2, 3, and 5 the model switched at one point in time, when all mature fish had organised in schools that had a size of at least 50 individuals. Designs 1 and 4 did not show a single switch event, but transitioned gradually by continuously aggregating schooling fish into school-agents. Finally, Design 6 was a special case: in this model, the switching entity was the plankton stock. It started in its aggregated stock design and it disaggregated to a spatial stock at the point when the amount of consumed plankton grew beyond a threshold that had the potential to entail heterogeneous conditions. The switch order was thus reversed in comparison to the other models.

6. Discussion

The presented simulation results showed large differences between model designs. As the same parameters were used for all designs, these differences could be attributed to the structure of the respective model design. In the following, we discuss the model designs with respect to their adequacy in capturing the modelled system versus their computational efficiency as well as potential information loss due to switching.

6.1. Considerations of space in dynamic hybrid designs

In the light of simulation results, we revisit the argument presented at the outset of this paper that the diverse and interwoven natural processes ideally are modelled with hybrid approaches (Heath et al., 2011; Laniak et al., 2013). The main challenge that comes with the greater flexibility of hybrid models is to find an adequate design. Although, the exemplary system in this paper consisted of only two populations with just one switch, there were 120 alternative ways to design the model. For the six most plausible designs that were implemented, simulation results differed greatly. Especially, it proved essential how the spatial context was considered in the model. Designs that did not account for spatial resource restrictions significantly overestimated fish population numbers by at least 45% (Designs 1 to 3). Additional disregard of spatial interactions between fish in the arrangement into schools (Designs 2 and 3) resulted in 70% larger populations compared to the spatially explicit design (Design 4). Omitting movement behaviour of fish in the spatial fish stock design (Design 5) limited the fish population to 15% compared to the representation of fish by school-agents in Design 4. Thus, this spatially explicit representation of fish by school-agents and plankton by spatial stocks resulted to be the most plausible design. This is further backed by the rough match of simulation results with the estimated value for the maximum

population size of 500,000 Alpine whitefish in Attersee (Wolfram and Miksch, 2007).

The presented school-agents in Design 4 relate to the concept of super-individuals introduced by Scheffer et al. (1995). These super-individuals averaged attributes and have been proposed as a computationally viable alternative to the explicit representation of single individuals (Scheffer et al., 1995; Parry and Evans, 2008). The approach was extended by Vincenot et al. (2011) and by Swinerd and McNaught (2012), who proposed to represent the rich internal structure of a super-individual by means of a SD model. Building on these hybrid super-individuals, we advanced the concept by introducing emergence-based reversible switches between individuals and super-individuals. We argue that super-individuals should be considered as potentially useful structural elements of a switching hybrid model that can link hierarchical and spatial scales, rather than only considering computational necessities.

6.2. Information loss due to switching

Although it proved potentially valuable, dynamic switching entailed issues of information loss. As the switching approach implies that any switch is reversible, the respective levels of detail were reconstructed at the cost of information loss. The six presented model designs were based on four different switch types, one for plankton and three for the fish population. Table 8 provides an overview of the switch types and the corresponding nature of information loss.

The first switch type triggered the change between plankton stocks and spatial plankton stocks in Design 6 (Agent/spatial stock – agent/stock). To minimise spatial information loss the aggregating switch was triggered, when the spatial plankton stocks showed a homogeneous distribution.

The second switch type was the aggregation of fish agents into a stock as realised in Design 3 (Agent/stock – stock/stock). With the loss of individual attributes, also the location of fish and their spatial distribution was lost through aggregation. However, the loss of information on individual attributes is minimised by the use of conveyor stocks. Unlike reservoir stocks, conveyors maintain arrival integrity (Richmond and Peterson, 2001). The distribution of age in the fish population was thus retained in daily bins. The loss of spatial information resulted in slightly different population dynamics in the fishing experiment. When the model switched back to its individual-based design, the location of fish were initialised randomly. After the reversed switch, it took time until fish had clustered again into schools. As school membership was a precondition for successful reproduction, growth was delayed and the probability of a population collapse increased. To avoid such effects due to randomised initialisations of the spatial distribution, Gray and Wotherspoon (2012) suggest to store spatial distributions as a basis to eventually restore individual locations. However, under conditions of population growth, the spatial distribution of fish changes as fish self-organise into schools. Therefore, storage of aggregated distribution is applicable primarily under stable system conditions.

The third switch type triggered aggregation of agents into spatial stocks as implemented in Design 2 (Agent/stock – spatial stock/stock) and Design 5 (Agent/spatial stock – spatial stock/spatial stock). Whereas spatial information was retained, information on individual attributes (e.g. sex and age of fish) was lost. Even more importantly, this switch type also implied a change from an agent-centred (Lagrangian) to a cell-centred (Eulerian) representation from which a fundamentally different representation of processes follows. As the processes of movement and dispersal were discontinued after the switch, the spatial fish stocks grew only in the cells that had been colonised at switch time.

Finally, the fourth switch type toggled between agents and school-agents. This switch type was implemented in Design 1

Fishing experiment: reversible model switching

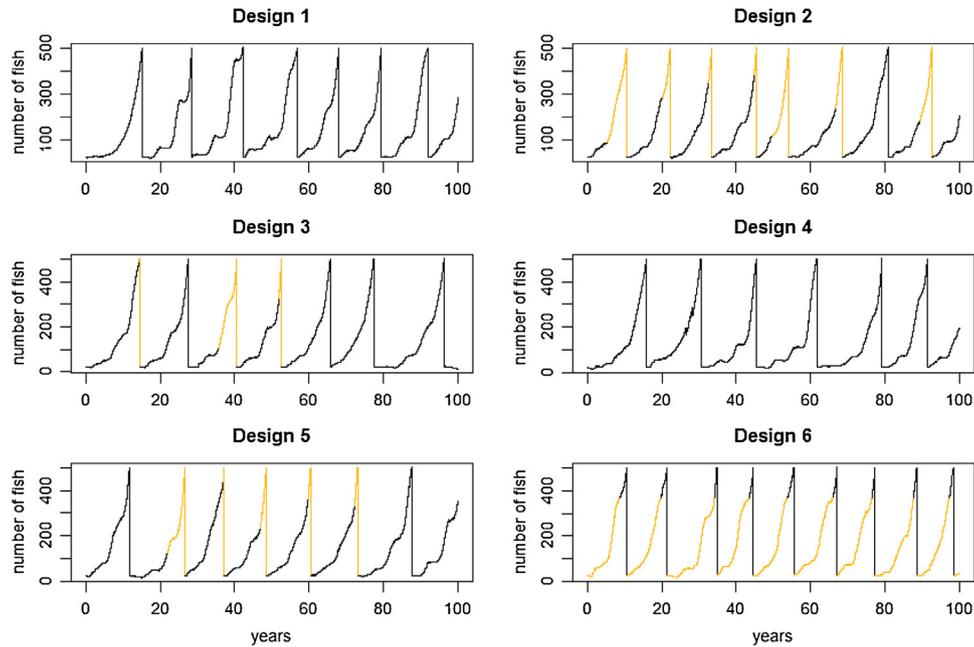


Fig. 5. The fish population dynamics in the fishing experiment shows dynamic switching between model configurations: Phases of disaggregated configurations are black, aggregate phases are brown.

Table 8

The nature of information loss due to switching.

Switch type	Model design	Information loss due to aggregation
Spatial stock → stock	Design 6	Loss of spatial information
Agent → stock	Design 3	Loss of individuality and loss of spatial information
Agent → spatial stock	Design 2, 5	Change from Lagrangian to Eulerian view
Agent → super-agent	Design 1, 4	Loss of individuality

(Agent/stock – school-agent/stock) and Design 4 (Agent/spatial stock – school-agent/spatial stock). The switch was triggered each time a new school has emerged, which resulted in a smooth transition rather than a hard switch. Spatial information as well as the Lagrangian perspective were retained, and information loss on individual attributes was minimised by the use of conveyor stocks. Therefore, the least information is lost in this switching type.

For all switches, the triggers operated similar to the scheduler that Gray and Wotherspoon (2012) used to mediate hybrid model switches under the overall goal of model efficacy. The main difference is that the scheduler in Gray and Wotherspoon (2012) is governed by an event that was independent of the population, whereas in the here presented models the switch was governed by the state of the represented populations themselves. This way, the representation of systems was optimised in terms of accuracy versus efficiency and the loss of information through switching was minimised. From the perspective of agent based modelling, emergence of higher-level features from individual entities is a main feature of bottom-up modelling. Therefore, the loss of detail does not necessarily involve loss of relevant information, when an emerged entity switches into an aggregated representation. This approach is in line with Gray and Wotherspoon (2015), who propose adaptive model structures in response to the model's state, and it complements approaches that are primarily governed by performance thresholds, as suggested by Vincenot et al. (2011) and Swinerd and McNaught (2012). In the presented models, the trigger is based on a simple set of descriptors, which extends the threshold-

approach suggested by Bobashev et al. (2007). The results of this research suggest negligible effects of the individual-based representation once sufficiently large and stable fish schools have emerged. Further research should explore more elaborate rules for the automatic detection of emergent features.

6.3. Computational performance and software

The general rule that a more precise model representation is more computational demanding, triggered research on optimising trade-offs between the computational and the predictive performance of a hybrid model (Vincenot and Moriya, 2011; Gray and Wotherspoon, 2012). In the presented models, the performance differed greatly, between 30 s for Design 3 and 1 h 58 min for Design 5. For Design 6, the 100-year simulation experiment could not be successfully executed due to the high computational burden during simulation. The observed exponential increase of elapsed time per time step in Design 6 is caused by a non-linear increase of interactions between agents as the number of agents increases.

Design 4 resulted in the most plausible results and at the same time experienced the least loss of information due to switching. Interestingly, Design 4 also performed second best with only 15 min processing time. This is surprising. First, because Design 1 should compute faster due to its more aggregate design. However, the shorter processing time can be explained with the lower number of agents in Design 4. Second, because one would expect that the spatial fish stocks in Designs 2 and 5 compute faster than the

school-agents in Design 4. An explanation may lie in the amount of computationally intensive conveyor stocks: whereas there were 1162 spatial plankton stocks in the lake, there were only about 110 school-agent stocks. The use of conveyor instead of reservoir stocks was also imposed by a limitation of the NetLogo software. Whereas it is widely used for agent-based modelling, NetLogo has only rudimentary functionalities for SD modelling. Specifically, the lack of a functionality to implement system delays had significant impacts on the computational model performance and hampered diagrammatic modelling, which are major strongpoints of SD.

7. Conclusions

In this paper we proposed a framework for adaptive and reversible switching between hybrid AB-SD model designs. To demonstrate the approach, we implemented six dynamic hybrid model designs for a predator-prey model of fish and plankton. The presented simulation results showed how emergence-based aggregation of individual agents to higher-level collectives can optimise the trade-off between predictive and computational modelling performance. Dynamic switching facilitated an adaptive response of the model structure to the emergence of fish schools. The best performing model design was a spatially explicit model. It was based on a switch between agents and school-agents for fish in combination with spatially discretised plankton stocks that were governed by a cellular automaton. Simulation results indicated that super-individuals can be adequately used as structural elements of dynamic hybrid models, which complements a primarily performance-oriented utilisation in the past. We argue that switches that are triggered by emergence can connect hierarchical and spatial scale levels, while minimising loss of relevant information. Surprisingly, some of the more aggregated models performed worse in terms of simulation processing times. Thus, we conclude that more suitable and spatially explicit model designs are not necessarily computationally inferior. Future research should be directed towards a rule-based identification of emergent phenomena to optimise switch timing and it further should support software development to overcome current shortcomings in multi-paradigmatic modelling functionality.

References

- Ahmad, S., Simonovic, S.P., 2004. Spatial system dynamics: new approach for simulation of water resources systems. *J. Comput. Civil Eng.* 18 (4), 331–340.
- Akkermans, H., 2001. Emergent supply networks: system dynamics simulation of adaptive supply agents. *System Sciences*, 2001. Proceedings of the 34th Annual Hawaii International Conference On, IEEE.
- Bobashev, G.V., Goedecke, D.M., Yu, F., Epstein, J.M., 2007. A hybrid epidemic model: combining the advantages of agent-based and equation-based approaches. *Simulation Conference*, 2007 Winter, IEEE.
- Borshchev, A., Filippov, A., 2004. From system dynamics and discrete event to practical agent based modeling: reasons, techniques tools. *Proceedings of the 22nd International Conference of the System Dynamics Society*.
- Brown, E.A.R., Finnigan, N., Scott, D.B.C., 1991. A life table for powan, *Coregonus lavaretus* (L.) in Loch Lomond, Scotland: a basis for conservation strategy. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 1 (2), 183–187.
- Dowlatabadi, H., 1995. Integrated assessment models of climate change: an incomplete overview. *Energy Policy* 23 (4–5), 289–296.
- Ecker, N., 2003. Die fischereiliche Bewirtschaftung des Attersees am Beispiel der Reinanke. In: *Thesis. Landwirtschaftskammer Oberösterreich, Seewalchen, Austria*, pp. 28.
- Einsele, W., 1942. Über das Wachstum der Coregonen im Voralpengebiet insbesondere über das Verhältnis von Schuppen- und Längenwachstum. *Zeitschrift für Fischerei* 41, 23–45.
- Froese, R., Pauly, D., 2016. *FishBase*.
- Gallagher, R., Appenzeller, T., Normile, D., Service, R.F., et al., 1999. Beyond reductionism. *Science* 284 (5411), 79–109.
- Gray, R., Wotherspoon, S., 2012. Increasing model efficiency by dynamically changing model representations. *Environ. Modell. Softw.* 30, 115–122.
- Gray, R., Wotherspoon, S., 2015. Adaptive submodel selection in hybrid models. *Front. Environ. Sci.* 3, 58.
- Grignard, A., Taillandier, P., Gaudou, B., Vo, D.A., Huynh, N.Q., Drogoul, A., 2013. *GAMA 1.6: Advancing the art of complex agent-based modeling and simulation*. *International Conference on Principles and Practice of Multi-Agent Systems*, Springer.
- Hamilton, S.H., ElSawah, S., Guillaume, J.H.A., Jakeman, A.J., Pierce, S.A., 2015. Integrated assessment and modelling: overview and synthesis of salient dimensions. *Environ. Modell. Softw.* 64, 215–229.
- Heath, S.K., Buss, A., Brailsford, S.C., Macal, C.M., 2011. Cross-paradigm simulation modeling: challenges and successes. *Proceedings of the Winter Simulation Conference Winter Simulation Conference*.
- Hofbauer, M., 2009. *Gewässerschutzbericht 43. Seenaufsicht in Oberösterreich*, 43. Amt der Oberösterreichischen Landesregierung, pp. 287.
- Kelly, R.A., Jakeman, A.J., Barreteau, O., Borsuk, M.E., ElSawah, S., Hamilton, S.H., Henriksen, H.J., Kuikka, S., Maier, H.R., Rizzoli, A.E., 2013. Selecting among five common modelling approaches for integrated environmental assessment and management. *Environ. Modell. Softw.* 47, 159–181.
- Kissman, C.E., Williamson, C.E., Rose, K.C., Saros, J.E., 2013. Response of phytoplankton in an alpine lake to inputs of dissolved organic matter through nutrient enrichment and trophic forcing. *Limnol. Oceanogr.* 58 (3), 867–880.
- Kuparinen, A., Stenseth, N.C., Hutchings, J.A., 2014. Fundamental population-productivity relationships can be modified through density-dependent feedbacks of life-history evolution. *Evol. Appl.* 7 (10), 1218–1225.
- Lättilä, L., Hilletoft, P., Lin, B., 2010. Hybrid simulation models –when why, how? *Expert Syst. Appl.* 37 (12), 7969–7975.
- Laniak, G.F., Olchin, G., Goodall, J., Voinov, A., Hill, M., Glynn, P., Whelan, G., Geller, G., Quinn, N., Blind, M., Peckham, S., Reaney, S., Gaber, N., Kennedy, R., Hughes, A., 2013. Integrated environmental modeling: a vision and roadmap for the future. *Environ. Modell. Softw.* 39, 3–23.
- Miller, I., Knopf, S., Kossik, R., 2005. Linking general purpose dynamic simulation models with GIS. In: Maguire, D.J., Batty, M., Goodchild, M.F. (Eds.), *GIS, Spatial Analysis, and Modeling*. CA ESRI Press, Redlands.
- Osgood, N., 2007. Using traditional and agent based toolsets for system dynamics: present tradeoffs and future evolution. *Syst. Dyn.*
- Parker, P., Letcher, R., Jakeman, A., Beck, M.B., Harris, G., Argent, R.M., Hare, M., Pahl-Wostl, C., Voinov, A., Janssen, M., Sullivan, P., Scoccimarro, M., Friend, A., Sonnenschein, M., Barker, D., Matejcek, L., Odulaja, D., Deadman, P., Lim, K., Larocque, G., Tarikhi, P., Fletcher, C., Put, A., Maxwell, T., Charles, A., Breeze, H., Nakatani, N., Mudgal, S., Naito, W., Osidele, O., Eriksson, I., Kautsky, U., Kautsky, E., Naeslund, B., Kumblad, L., Park, R., Maltagliati, S., Girardin, P., Rizzoli, A., Mauriello, D., Hoch, R., Pelletier, D., Reilly, J., Olafsdottir, R., Bin, S., 2002. Progress in integrated assessment and modelling. *Environ. Modell. Softw.* 17 (3), 209–217.
- Parry, H.R., Evans, A.J., 2008. A comparative analysis of parallel processing and super-individual methods for improving the computational performance of a large individual-based model. *Ecol. Modell.* 214 (2–4), 141–152.
- Phelan, S.E., 1999. A note on the correspondence between complexity and systems theory. *Syst. Prac. Action Res.* 12 (3), 237–246.
- Reynolds, C.W., 1987. *Flocks, Herds and Schools: A Distributed Behavioral Model*. ACM Siggraph Computer Graphics. ACM.
- Richardson, K.A., Midgley, G., 2007. Systems theory and complexity: part 4 – The evolution of systems thinking. *E:CO* 9 (1/2), 166.
- Richmond, B., Peterson, S., 2001. An Introduction to Systems Thinking, Featuring STELLA. High Performance Systems Incorporated.
- Salter, R.M., 2013. *Nova: a modern platform for system dynamics, spatial, and agent-based modeling*. *Procedia Comput. Sci.* 18, 1784–1793.
- Schaber, P., 1985. Das Nährstoffpotential des zooplanktons in österreichischen gewässern. *Österreichs Fischerei* 38, 57–64.
- Scheffer, M., Baveco, J.M., DeAngelis, D.L., Rose, K.A., van Nes, E.H., 1995. Super-individuals a simple solution for modelling large populations on an individual basis. *Ecol. Modell.* 80 (2), 161–170.
- Schieritz, N., Milling, P.M., 2003. Modeling the forest or modeling the trees. *Proceedings of the 21 St International Conference of the System Dynamics Society*.
- Scholl, H.J., 2001. Agent-based and system dynamics modeling: a call for cross study and joint research. *System Sciences*, 2001. Proceedings of the 34th Annual Hawaii International Conference On, IEEE.
- Shanthikumar, J.G., Sargent, R.G., 1983. A unifying view of hybrid simulation/analytic models and modeling. *Oper. Res.* 31 (6), 1030–1052.
- Sibly, R.M., Grimm, V., Martin, B.T., Johnston, A.S., Kułakowska, K., Topping, C.J., Calow, P., Nabe-Nielsen, J., Thorbek, P., DeAngelis, D.L., 2013. Representing the acquisition and use of energy by individuals in agent-based models of animal populations. *Methods Ecol. Evol.* 4 (2), 151–161.
- Stemate, L., Pasca, C., Taylor, I., 2007. A comparison between system dynamics and agent based modeling and opportunities for cross-fertilization. *Simulation Conference*, 2007 Winter, IEEE.
- Swinerd, C., McNaught, K.R., 2012. Design classes for hybrid simulations involving agent-based and system dynamics models. *Simul. Modell. Pract. Theory* 25, 118–133.
- Tolonen, A., 1998. Application of a bioenergetics model for analysis of growth and food consumption of subarctic whitefish *Coregonus lavaretus* (L.) in Lake Kilpisjärvi, Finnish Lapland. *Hydrobiologia* 390 (1), 153–169.
- Vincot, C.E., Moriya, K., 2011. Impact of the topology of metapopulations on the resurgence of epidemics rendered by a new multiscale hybrid modeling approach. *Ecol. Inf.* 6 (3), 177–186.
- Vincot, C.E., Giannino, F., Rietkerk, M., Moriya, K., Mazzoleni, S., 2011. Theoretical considerations on the combined use of System Dynamics and individual-based modeling in ecology. *Ecol. Modell.* 222 (1), 210–218.

Voinov, A., Shugart, H.H., 2013. 'Integronsters', integral and integrated modeling. *Environ. Modell. Softw.* 39, 149–158.

Wilensky, U., 1998. NetLogo Flocking Model. Center for Connected Learning and Computer-Based Modeling, Northwestern University, Evanston, IL.

Wilensky, U., 1999. NetLogo. Center for Connected Learning and Computer-Based Modeling Northwestern University, Evanston, IL.

Wolfram, G., Mikschi, E., 2007. Rote Liste Der Fische (Pisces). Böhlau-Verlag, Österreichs Wien, Köln, Weimar.