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The confluences of ideas leading to, and the flow of ideas emerging from, individual-based modeling of riverine fishes

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Abstract

In this review article, we trace the history of events leading to the development of individual-based models (IBMs) to represent aquatic organisms in rivers and streams. As a metaphor, we present this history as a series of confluences between individual scientists sharing ideas. We describe contributions of these models to science and management. One iconic feature of river IBMs is the linkage between flow and the physical habitat experienced by individuals, and the first model that focused on this linkage is briefly described. We continue by reviewing the contributions of riverine IBMs to eight broad areas of scientific inquiry. The first four areas include research to understand 1) the effects of flow regimes on fish populations, 2) species interactions (e.g., size-mediated competition and predation), 3) fish movement and habitat selection, and 4) contaminant and water quality impacts on populations. Next, we review research using IBMs 5) to guide conservation biology of imperiled taxa through population viability analysis, including research 6) to understand fragmentation and reconnection, 7) to understand genetic outcomes for riverine metapopulations, and 8) to anticipate the future effects of temperature and climate change. This rich body of literature has contributed to both theoretical insights (e.g., about animal behavior and life history) and applied insights (e.g., population-level effects of flow regimes, temperature, and the effects of hydropower and other industries that share rivers with aquatic biota). We finish by exploring promising branches that lie ahead in the braided channel that represents future river modeling research.

We dedicate this paper to Dr. Webster Van Winkle, who passed away March 29, 2018. Webb was a facilitator of, and pioneer in, IBM modeling and coauthor of the first IFIM-type river IBMs.

1. Individual confluences passing streams of memes

Ideas in science rarely emerge intact. Rather the conditions leading to new ideas or 'memes' spring up in different places and follow independent paths that then converge, merge, and spread. This was true for individual-based modeling (IBM), and later, the development of IBMs for biota in rivers and streams. Ideas flowing out of tributaries carried advances in computer science, theoretical ecology (e.g., optimal foraging theory), forest-gap modeling, and physical modeling of dynamic stream habitat.

These ideas co-mingled to generate a diverse, braided complex of downstream channels that continues to bring new insights (Figure 1). These downstream channels are different in size. A large productive inSTREAM modeling community of users is an important example. In addition, the initial EPRI models fed into genetic IBMs (IBM+G) and other variants and these have been used to address a wide variety of basic and applied scientific questions.

[Figure 1]

The use of individual-based modeling in ecology, as depicted in Figure 1, emerged initially at the confluence between silvicultural problems (one tributary branch) and technological progress (another tributary) in the early 1970's. The technological advance was the increasing power of computers, while the motivating problems involved how to optimize planted forests; e.g., what trees to plant, and how to space them (Shugart et al., 2018; Shugart and Woodward, 2011). Computational power allowed Yale ecologist Daniel Botkin to model a forest in the way that he thought it really worked mechanistically. Working with James Wallis and James Janak of IBM's Thomas J. Watson Research Center, Botkin simulated the growth of individual trees of different species as accurately as possible, given their basic traits and local soil and climate conditions, and then let trees from different species interact on a small plot through mutual competition for light. This general type of model was termed an 'individual-based model', or, coincidentally, IBM.

JABOWA was called a ‘gap-phase replacement’ model because the spatial area simulated was about the size of a gap left by the death of a large canopy tree (Botkin et al., 1972). JABOWA predicted the successional dynamics of tree communities in a New Hampshire forest so well that forest ecologists such as Bormann and Likens (1979) used it to derive their ideas about biomass accumulation in aggrading forests. Hank Shugart and Darrell West, then research ecologists at Oak Ridge National Laboratory, soon developed a version of a gap-phase replacement IBM named FORET (Shugart and West, 1977) and other models followed, as reviewed by Bugmann (2001). By now scores of different forest simulation platforms with a high degree of detail and sophistication exist and are applied world-wide.

Two factors made fish the next candidate for extensive application of individual-based modeling. The first factor is that individual size is an important characteristic for piscivorous fish, as it was for trees. As gape-limited predators, size influences the foraging success of fish and their ability to escape predation by other fishes. Individual differences in size within a cohort could therefore influence the dynamics of that cohort. DeAngelis et al. (1980) demonstrated this for a cohort of young-of-the-year largemouth bass (*Micropterus salmoides*) in an aquarium. Depending on the initial size distribution, varying degrees of cannibalism could occur within the cohort, leading to a final number of surviving fish after a couple of months. The IBM, which followed every fish in the cohort through time, was able to predict the outcomes of two successive aquarium experiments surprisingly well.

The second factor favoring development of IBMs for fish was the need to understand the effects of mortality of fish though entrainment and impingement by nuclear power plant cooling systems (Figure 1). A key question was to what extent compensatory mechanisms in the fish populations could mitigate the loss of perhaps billions of eggs, larval, and other early life-stage fish. At high densities, few offspring of such species survive to adulthood due to density-dependent mortality. The loss of some fish by non-natural factors such as power plants increases resources available to others. Therefore, increased mortality imposed by anthropogenic sources was proposed by some scientists to have little net effect on recruitment to the adult stage.

To understand and quantify how such compensatory mechanisms work in fish populations, the Electric Power Research Institute (EPRI) funded a 10-year project, “Compensatory Mechanisms in Young-of-the-Year Fish”, at Oak Ridge National Laboratory (ORNL), which already had a long history of studying the effects of power plants on fish (Barnthouse et al., 1984; Boreman et al., 1981; Coutant, 1971). The project, led by Dr. Webster Van Winkle and stimulated by the success of IBM forest simulations by colleagues at ORNL, used the IBM approach to try to understand the complex processes of growth and mortality of young-of-year (YOY) fish of species potentially impacted by nuclear power plants. At universities across North America, PhD students funded by EPRI developed such models, in the process training a generation of fish ecologists in modeling. Following the ‘Wisconsin’ school of fish modeling, the bioenergetics of each fish was modeled in these IBMs, and large numbers of young-of-year fish were simulated, along with food resources and predation, to estimate the effects of power plants and other mortality factors. Early papers were published by DeAngelis et al. (1990), Madenjian et al. (1991), and Deangelis et al. (1991) for fish in lakes. DeAngelis et al. (1993) predicted patterns of recruitment vs. egg density and the transition from density-dependent to density-independent mortality in YOY fish that agreed well with empirical patterns. Scheffer et al. (1995) introduced the key IBM modeling technique of ‘super individuals’ to efficiently simulate huge numbers of YOY, most of which die in the first year of life. Applications of IBMs to fishes were reviewed by (VanWinkle et al., 1993) and more recently by Sibly et al. (2013). The growth in IBMs during the late 1980s in all areas of ecology and across taxa stimulated both a review paper of individual-based modeling in general (Huston et al., 1988) and a workshop at the University of Tennessee in 1990, published as a proceedings (DeAngelis and Gross, 1992, editors). In a subsequent review, (DeAngelis and Mooij, 2005) counted over 900 manuscripts using IBMs, over 100 of which were applied to fish, though these numbers were surely underestimates. The monograph of Grimm and Railsback (2005) advanced the theoretical foundations for individual-based modeling.

Modeling of individual activities was influenced by bioenergetics modeling (e.g., the 'Wisconsin' school for fishes, mostly centered on lake fishes), optimal foraging theory, and theories related to habitat selection and movement (Figure 1). These component sub-models used to represent individual activities formed the backbone of IBMs. Other early papers described IBMs of riverine populations. (Petersen and Deangelis, 1992) simulated northern pike fish (formerly squawfish, *Esox lucius*) predation on juvenile salmon, addressing the question of how schooling of downstream swimming smolts reduced predation risk in a Columbia River reservoir, and Rose and Cowan (1993) simulated striped bass in the Potomac River.

Arguably, river IBMs differ from those applied to organisms in other ecosystems because the dynamic and directional changes in river habitat are such an important influence on species' life histories. Thus, the ability to simulate population-level responses to flow as an outcome of individual behaviors is a defining characteristic, and development of river IBMs depended on the convergence of two tributary ideas. One tributary carried the biological IBM and the other carried the Instream Flow Incremental Methodology or IFIM (Orth and Maughan, 1982). Used to establish minimum flows for fishes below dams in the United States, the IFIM has two components; (1) physical habitat modeling (for the variables depth, velocity, and cover) and (2) representation of species preferences for these three habitat variables (Bovee, 1982; Thomas and Bovee, 1993). Because preference curves are not flow-invariant and do not necessarily reflect a species' habitat requirements over time well, the IFIM generated controversy from its inception (Mathur et al., 1985; Railsback, 2016). In the confluence of the 1980s, Dr. Mike Sale, a recently-hired environmental engineer, brought his experience with IFIM models to Oak Ridge, where he recognized the potential for applying IBMs in river ecosystems. The confluence of ideas among theoretical modelers, environmental engineers, and aquatic ecologists in East Tennessee spawned many uses of IFIM models using IBMs to study riverine fishes. These tools have produced numerous insights, not just in understanding flow responses by fishes and reducing uncertainty in instream-flow standards (VanWinkle et al., 1997), but also in understanding biological processes. Below we will highlight aspects specific to lotic habitats.

Over the years, individual- or agent-based modeling has evolved (DeAngelis and Grimm, 2014). For example, computation times were reduced through the use of various 'cloning' methods for representing meta-individuals started to be used (Rose et al., 1993). An attractive feature of IBMs as mechanistic process-based models is the ability to 'validate-by-parts' and to compare against intermediate outputs. New techniques were adopted for model-data comparison. One is to compare patterns produced by the model against those observed (e.g., the use of pattern-oriented model evaluation (Grimm and Railsback, 2012; Grimm et al., 2005), which is similar to 'functional validation' (Jager et al., 2000). The pattern-oriented approach can be used to select among alternative model structures that differ in complexity. A protocol for documenting IBMs was developed (Grimm et al., 2010). In addition, significant advances have been made in developing new methods for incorporating historical data and producing a distribution of model outcomes from a likelihood-weighted joint distribution of input parameters [e.g., approximate Bayesian computational methods (Piou et al., 2009)]. Developments specific to riverine IBMs include alternative approaches to representing dynamic stream habitat (hydrodynamics, stream temperature and water quality), simulation of animal movement in a directional flow environment, and models that use network theory as a basis for representing dendritic riverine metapopulations. These advances are described in the sections below.

In this paper, we trace the ideas leading to modeling of river fish populations using IBMs, we highlight some of the key contributions IBMs have made to understanding aquatic populations in river habitat, and we suggest future opportunities for new discoveries.

2. Headwaters of riverine IBMs

One of the first IBMs applied to riverine populations in the early 1990's sought to understand the effects of regulated flow regimes on fish in the North Anna River, Virginia, USA. The model, focused on smallmouth bass (*M. dolomieu*), was published in the journal, *Rivers*, that is no longer in existence (Jager et al., 1993)(see Supplemental Information). This model evolved from a version developed by Deangelis et al. (1991) for lakes (Figure 1). The lake model simulated gape-limited optimal foraging on a spectrum of invertebrate (e.g., zooplankton) prey, ontogenetic size-based shifts in optimal diet, smallmouth bass bioenergetics, as well as nesting and reproduction.

To represent fish in a river environment, other processes became important to include. Representation of physical habitat linking time series of flow and temperature to 2-dimensional fields of depth and velocity, and the responses of each biological process to those fields is depicted in Figure 2 and described below.

[Figure 2]

Physical habitat. Flow is such an important driver of habitat for fishes and other river biota that much more attention to dynamic simulation of habitat was required. This was achieved by coupling hydraulic simulation portion of the Physical Habitat Simulation System (PHABSIM) directly with an individual-based model for nesting, reproduction, and YOY dynamics (Figure 2). To represent hydrodynamics, the data requirements were significantly higher than those of previous IBMs. PHABSIM relies on measurements of depth and velocity along fixed transects at different flows, as well as substrate and cover. A representative stream reach was partitioned into spatial cells containing measurement stations from a PHABSIM survey of the reach. The model required daily predictions of average depth and velocity for each grid cell in the representative reach as a function of daily average flow (Figure 2). In later models, changes in velocity with depth and presence of cover were represented as well (Van Winkle et al., 1998). Water temperature was also simulated, influencing fish growth and development.

Movement. The smallmouth bass IBM uses departure rules to simulate fish movement (Jager and Tyler, 2001). Each individual fish's growth over time is tracked. In a time-for-space substitution, movement is initiated when growth falls below the fish's long-term expectation.

Foraging. Foraging differs substantially in flowing rivers compared with lentic habitats. Regeneration of prey is affected by flow, and by the local habitat's carrying capacity, setting an upper limit on standing biomass. Larger invertebrate prey items and crayfish are simulated because these can be important in streams, especially for larger bass. The model was able to reproduce fish growth in the North Anna River.

Mortality. Mortality factors in rivers and streams differ from those in lakes because of the risk of being swept away by high flows or dewatered during non-mobile life stages (i.e., eggs and larvae during nesting). One insight produced from this river IBM is a recognition that non-mobile life stages are the most vulnerable when examining responses to disturbance regimes.

Reproduction. Reproduction and early development are affected by different abiotic effects in rivers than they are in lakes. Nesting and guarding of nests by males were represented in both the lake and versions of the model. However, to understand nesting success in dynamic rivers, it is important not only to simulate disturbance of nests by flow extremes (e.g., floods or dewatering), but also to provide the opportunity for renesting if disturbance is early in the season. We compared simulated reproductive success and first year growth with field observations from the North Anna River in Virginia. The timing of nesting was well-simulated based on water temperature (see Supplemental Information), and renesting occurred on three occasions in 2-year simulations.

In summary, this first IBM linking river habitat dynamics to fish populations explored previously unappreciated facets of riverine fish responses and adaptation to flow. But more importantly, it laid the groundwork for subsequent modeling efforts to evaluate the influence of alternative flow regimes, as the authors continued to deploy river IBMs, with the next applications focused on trout (Van Winkle et al., 1998) and Chinook salmon (Jager et al., 1997), as well as numerous others reviewed below.

3. How have river IBMs contributed to ecology?

Since the early models described above, river IBMs have fanned out to address a varied set of questions, illustrated by the braided channel in Figure 1, yielding different kinds of insights. Spatially explicit IBMs are well-suited for many questions involving aquatic populations in river habitats for several reasons. First, as noted by Anderson et al. (2013b) properties that emerge from transient, non-equilibrium dynamics are particularly important in disturbance-dominated ecosystems like rivers (Strange et al., 1993). Second, risks are dependent on attributes of individuals. In addition to size-dependent predation risk, in regulated rivers, entrainment and survival of turbine passage both depend on fish size.

HIJ conducted a Web of Science search of "individual-based model" in the title and ('river' OR 'stream'), which found 54 publications, with an average of 25 citations per publication. When 'individual-based' was not required to be in the title, and extraneous topics were excluded, just under 200 papers were identified between 1992 and 2018 and these produced an average of 36.2 citations per item. The number of publications increased near-linearly over time. Many of these publications were produced by a few individuals (Dr. Steve Railsback, with coauthor Dr. Brett Harvey authored 8.2 and 7.1% of papers based on the InSTREAM model). Other authors represented many countries, with more than half from the USA, roughly 10% each from England, Canada, and France, followed by Germany, the Netherlands, China, Japan, and Norway and twelve other countries. Papers were published in the journal Ecological Modeling (16%), fisheries journals (28%), and general ecology and conservation journals (16%), especially PLOS One and Ecological Applications, with the remaining journals represented by fewer than two papers each. Two studies were published in the Proceedings of the National Academy of Sciences, USA.

Processes in rivers, as in most ecosystems, span multiple scales (Anderson et al., 2005). Likewise, riverine IBMs with different purposes fall along a range of scales from a focus on spatial questions related to fish responses to flow- and temperature-mediated variation in habitat (lower left in Figure 3) to questions related to metapopulation dynamics in river networks (upper right in Figure 3).

[Figure 3]

The specific questions which river IBMs have been used to address (Figure 5) have evolved over time, but at least one general purpose (e.g., understanding the effects of river regulation) has remained an active area of research throughout. One significant shift in emphasis has been from models to manage stream habitat for fisheries to Population Viability Analysis (PVA) models designed to guide recovery of rare species of high conservation concern. Below, we briefly discuss four categories of IBM studies focused on single tailwaters or reaches in which higher spatial resolution is used (bottom left in Figure 3) and four categories of IBM modeling studies involving long-term projections of meta-populations over broader spatial scales (upper right portion of Figure 3). These studies relate to the questions depicted in Figure 4.

[Figure 4]

3.1 Research to understand the effects of flow regimes on fish populations

Understanding how flow regimes influence fishes is a fundamental area of river research has been, and continues to be, explored by IBMs (Figure 6a). From an early emphasis on determining ‘how much flow a river needs’ through setting minimum flow standards, to the more-recent emphasis on flow variability, a mechanistic understanding of the linkages between flow regimes is needed, and spatially explicit IBMs provide this capability. Some of the more recent research is described in section 3 under 'Research to understand habitat selection and movement'. The purpose of early river IBMs was to improve the 'fish preference' curves used in IFIM. Although IFIM is typically used in a regulatory context to set minimum flows, IBMs made it possible to address questions about flow regimes. For example, optimization flow releases from reservoirs was used to benefit downstream fishes, such as Chinook salmon (*Oncorhynchus tshawytscha*) (Jager and Rose, 2003). A key finding has been that thermal effects tend to have more biological importance than those of flow alone (Jager et al., 1997) (Tyler and Rutherford, 2007; Xu et al., 2010). In addition, IBMs have enabled researchers to evaluate the mechanisms behind ecological riverflow (i.e., properties of flow regimes including variation in flows) that benefit tailwater fish populations (Tyler and Rutherford, 2007) as well as ways in which 'natural flows' can be improved on. For example, one [non-IBM] study found that timing of releases earlier in spring than the natural snow-melt pulse produced floodplain inundation that allowed juvenile salmon to grow faster and exit the system before river temperatures became dangerously warm (Jager, 2014). Thus, an 'unnatural' flow regime performed better than the way that the river was historically regulated, which usually produced suboptimal flows for fishes.

[Figure 5]

Moving from an initial focus on setting minimum flow regulations, river managers now also focus on understanding elements of flow regimes that have high ecological value, and these are often the seasonal pulse flows (for example produced by snowmelt) to which native species are adapted in temperate rivers. In regulated rivers, flow augmentation ensures that high flows are available to downstream biota when needed. These pulse flows may facilitate migration and improve temperatures below dams. For example, cold, augmentation flows from Dworshak Reservoir are an important part of a strategy to facilitate salmon and steelhead migration through the hydrosystem of the lower Columbia River in spring. Augmentation may also be needed to provide flow in cases of extreme dewatering. In a more-arid climate, Pine et al. (2017) used a population viability analysis (PVA) IBM model to evaluate the potential benefits of augmenting flows to two federally-listed fish species in an arid New Mexico, USA stream.

Another important research area for regulated rivers is to understand trade-offs between operating in 'peaking' or 'load-following' mode, whereby flows are released when electricity demand (and value) is high. Rapid fluctuations in flow can have adverse effects on biota, and these can be modeled by IBMs that simulate influences on bioenergetics and on non-mobile life stages. For example, an IBM of the Green River below Flaming Gorge Dam predicted the effects of flow fluctuations on nursery habitats of the Colorado pikeminnow (*Ptychocheilus lucius*) (Grand et al., 2006).

3.2 Research to understand species interactions

IBMs can be used effectively to study species interactions (Figure 6b). For example, the spread of invasive aquatic species is a significant threat to native species worldwide, and one associated with human activity (Leprieur et al., 2008). Stream IBMs can be used to understand biologically mediated invasion dynamics. For example, topological properties of river networks and the spatial distribution of larval habitat within them controlled the spread of sea lamprey (Neeson et al., 2012).

The use of an IBM is particularly important when individual characteristics influence the outcome of such interactions. For example, representing individual size differences among fishes was an early emphasis because it highlighted the role of size-based (gape-limited) predation (Rice et al., 1993). Size was also the focus of the first application of an IBM to fish stocking, as resource managers became aware that releasing fish at a larger size could enhance survival (Madenjian et al., 1991). In situations when spatial resources can be defended (e.g., drift-feeding territories, high-quality spawning habitat), size-based competition for space occurs. This has been represented in models for salmonids. Similarly, competition for mates and female fecundity are functions of size or condition (Van Winkle et al., 1998).

The need to grow beyond a certain size prior to a stressful period (e.g., winter), and the population resilience created by 'contest' competition and compensatory (density-dependent) mortality were two insights gained through individual-based modeling (DeAngelis et al., 1993). In rivers, the first application with a focus on size-mediated effects simulated predation on migrating salmon smolts (Petersen and Deangelis, 1992, 2000). These size-based algorithms were later incorporated into models of bass predation on salmon juveniles in rivers, particularly deep pools (Jager et al., 1997). The interaction between warming rivers and predation by warm-water fishes on cold-water salmonids remains an important concern for species listed under the Endangered Species Act in rivers of the western US.

Trophic dynamics in rivers have been represented by IBMs (Anderson et al., 2012; Giacomini et al., 2009; Railsback and Harvey, 2013; Robson et al., 2017). Simulating predation required some changes when applied to species in flowing rivers. In lentic habitats, modelers typically assume that the geometry defined by the reaction distance of the fish and its speed define a cylindrical volume of pelagic prey, or a truncated volume of benthic prey, available to foraging fishes. In rivers, a strategy of 'sit-and-wait' drift feeding becomes possible (Fausch, 2014). Therefore, at low and high velocities, individuals are predicted to adopt a search strategy, whereas at intermediate velocities, profitability of a drift-feeding strategy is higher (Van Winkle et al., 1998). Another consideration is the relationship between flow and turbidity for visual-feeding fishes. Increased turbidity can lead to reduced feeding and subsequent starvation (Harvey and Railsback, 2009).

3.3 Research to understand fish movement and habitat selection

One of the most important reasons for adopting an individual-based approach is the need to represent movement at a relatively fine resolution (i.e., multiple reaches or patches within reaches versus a few different habitats). Understanding animal behavior (Figure 6c), including movement and habitat selection, has been studied by postulating and testing movement rules (Rohlf and Davenport, 1969), and this was greatly facilitated by using IBMs. This research was initially influenced by the wealth of literature in ecology on optimal foraging theory and decision rules for switching prey and habitat departure. Economic concepts, such as the marginal value theorem, were used in deciding when model organisms should leave a patch when searching for food (or other resource) (Rashleigh and Grossman, 2005; Tyler and Brandt, 2001). Early stream IBMs partitioned the day into resting and foraging portions, based on reaching a maximum daily ration within daylight hours (Van Winkle et al., 1998). An individual's departure from a patch was simulated to occur when its expectation of a higher ratio of growth to predation risk (or product of growth and survival) exceeded the value in the current stream cell (Jager et al., 1993; Railsback and Harvey, 2002; Van Winkle et al., 1998). Later models have identified situations in which the distribution of individuals does not reflect the fitness landscape, as is expected under an 'ideal-free distribution' produced by departure rules that optimize fitness (Railsback et al., 2003). The limited perceptual ability of individuals to sense conditions beyond their current location is one factor that can negatively influence the ability of a population to produce a distribution that tracks the fitness landscape (Jager and Tyler, 2001; Pe'er and Kramer-Schadt, 2008; Railsback et al., 1999, 2001).

Understanding movement is not merely a theoretical exercise. The use of spatially explicit IBMs can help resource managers by providing more-sophisticated movement algorithms to understand how management decisions influence fish populations (Railsback, 2016). In one example, simulation of flow responses by two carp species in China suggested relatively little effect of regulation, but did suggest improved timing of reservoir water releases during spring (Li et al., 2010). Understanding the effects of dams on downstream migration by juvenile salmon has been a strong area of applied research in the Columbia River Basin, where a large proportion of US hydropower is generated. Computational fluid dynamics has been used to understand juvenile salmonid movements through passage facilities (Gao et al., 2016; Romero-Gomez and Richmond, 2014; Weber et al., 2006). Typically, a combined Eulerian-Lagrangian-Agent (ELAM) approach (i.e., fish trajectories modeled through a fixed gridded physical habitat representation of a river) is employed (Goodwin et al., 2006). A hypothesis to explain the navigation of juvenile salmonids downstream through surface collectors and other devices at dams was the strain-velocity-pressure hypothesis, whereby juveniles are assumed to minimize total hydraulic strain (Nestler et al., 2008). This hypothesis has since been supplanted, as water acceleration alone appears to do a better job of predicting the movements of salmon. The resulting models simulate the ability of salmon to navigate safely through passage routes at large dams by modulating their swimming orientation and speed to water acceleration (Goodwin et al., 2014). The ELAM model differs from earlier PHABSIM models in that fish are simulated on a dynamic habitat represented by high-resolution computational fluid dynamics models (Weber et al., 2006).

The approaches above make sense for animals that can control movements. However, for some species and life stages, movement is passive and determined by flow fields. Fonseca (1999) used an IBM to examine the consequences of movement rules related to drift of blackfly larvae in a fluid medium and was able to reproduce spatial patterns of settling in depositional zones. In fragmented rivers, downstream drift of larvae was found to be an important effect on upstream population persistence. Thus, the most vulnerable life stages are those that are incapable of directed movement, whether because they are sessile (eggs, mussels) or because they lack apparatus for swimming well.

One situation where IBMs suggest that passive drift can be important is in coastal rivers, where salinity can play a role in movement and survival of early life stages that are not-yet salt-water tolerant (Jager et al., 2013a; Rose et al., 2014). Premature exposure to salinity was a leading cause of mortality for juvenile shortnose sturgeon (*Acipenser brevirostrum*) in an IBM for a river in coastal, Georgia, USA (Jager et al., 2013a). If confirmed by fieldwork, this risk will increase as sea level rises. Canals and water diversions can also influence exposure to high salinity in coastal rivers, as can intrusion of saltwater due to excessive groundwater pumping.

3.4 Research to understand contaminant and water quality impacts

One important ecosystem service provided by rivers is to transport and purify waste water from watersheds that support human activities. Riverine populations are affected along the way, and the population-level effects of individual exposure to contaminants and poor water quality have been quantified by using IBMs (Figure 6d). As stochastic models, IBMs represent realistic variation in exposure. Research in this area involves linking IBMs with dynamic and spatial models of water quality, and past examples have focused on reservoirs. For example, in the US, particle-based (Lagrangian) approaches have been used to simulate fish movements in a 2-dimensional reservoir (Nestler et al., 2002; Scheibe and Richmond, 2002). Blueback herring, *Alosa aestivalis*, were simulated in Strom Thurmond Reservoir in the southeastern US by using rules to simulate swimming in the direction of optimal habitat quality (Nestler et al., 2002). Reservoir habitat was represented by a laterally averaged CE-QUAL-W2 model of hydrodynamics, temperature, and dissolved oxygen (Nestler et al., 2002). Nestler et al. (2002) adjusted the parameters of conditional movement rules to produce reasonable seasonal responses. In another particle-based model, a vertically-averaged representation of a reservoir was used to evaluate exposure of juvenile salmon to dissolved gases while migrating near the water’s surface through dams on the Columbia River (Scheibe and Richmond, 2002). Sullivan et al. (2003) used a Eulerian approach to simulating movements of white sturgeon, *A. transmontanus*, in response to dissolved oxygen and temperature in the bottom layer of a Snake River reservoir. Two studies of fish movements have pointed to interactions between predation and dissolved oxygen. In one study, juveniles were spatially concentrated and therefore increasingly vulnerable to predation (Breitburg et al., 2003). Another study of simulated movement indicated how, depending on its location, hypoxia can create a barrier in reservoirs, as well as an 'ecological sink' for scavengers attracted to carcasses (Sullivan et al., 2003). Survival estimates for individuals produced by these IBMs can then be used to project population-level responses.

A handful of studies have used IBMs to evaluate contaminant effects at the population level and a few examples pertain to rivers. Salice et al. (2011) evaluated alternative strategies for Polychlorinated Biphenyl (PCB) cleanup on mink. The study determined that early cleanup was the best option. A study to rank threats to shortnose sturgeon used an IBM to evaluate risk from mercury (Jager et al., 2013b). Recently, Dohmen et al. (2016) compared toxicity from farm chemicals in ditches at the edge of a field using models representing hydrodynamics as a moving stream versus a deep pool. In shallow waters, toxicity was found to be higher primarily because of higher temperatures. Another comparison found drift in flowing waters to have an influence on population recovery (Van den Brink et al., 2007). In another recent example, Brito et al. (2017) evaluated sewage treatment options to select one most likely to protect the silver catfish (*Rhamdia quelen*).

The considerable research on contaminant transformation, fate and transport within rivers, floodplains, and reservoirs has not been married with the mechanistic power of river IBMs to aggregate individual-level exposure and effects to the population-level for riverine species. The studies above did not simulate detailed adverse outcome pathways experienced by individuals. To this end, a working group hosted by the National Institute for Mathematical and Biological Synthesis is currently evaluating ways to combine Dynamic Energy Budget (DEB) models with IBMs to scale the effects of contaminant exposure to understand effects at the population-level (Forbes et al., 2016).

3.5 Research to understand the conservation biology of rare fishes and other taxa

Perhaps it is ironic that understanding density dependence and compensatory mechanisms led to the development of IBMs for fish populations, because applications to understand threats to rare or endangered species are now more prominent (Peterseni et al., 2008). At the low end of the population density spectrum, Allee effects are as important as compensatory effects at high densities when developing IBMs for small populations. In conservation biology, questions about minimum population sizes for persistence emerge, and this is related to the question of whether there is sufficient habitat to support a viable population. In advective river environments, downstream drift is a dominant feature that influences population persistence (Kolpas and Nisbet, 2010). Generally speaking, species evolve spatial life histories that counteract this tendency. Fragmentation by dams can interrupt 'conveyer-belt' life histories characteristic of rivers and prevent access to the variety of habitat required to sustain viable populations.Therefore, assessing long-term viability involves understanding spatial metapopulation structure and mechanisms by which genetic structure is maintained.

An important use of PVAs is to rank threats to small populations (Caughley, 1994)(Figure 6e). IBMs used for PVA accomplish this by comparing scenarios with different assumptions about potential threats (Loos et al., 2010; Peterseni et al., 2008). The response variables in PVA's are those associated with population recovery; i.e., the likelihood of extirpation (or persistence), population trends, spatial diversity, and genetic diversity. Therefore, genetic models are appropriate. For example, an IBM+G PVA model was developed to rank risks linked to white sturgeon (*A. transmontanus*) populations in the middle Snake River (Jager et al., 2007). PVA studies typically require summarizing results from a large number of replicate [meta]populations and projecting many generations into the future. The combination of simulating many individuals and running Monte Carlo simulations is a significant computational challenge.

Applications of IBMs in conservation biology is especially important for river species because freshwater ecosystems contain some of the most imperilled taxa (Dudgeon et al., 2006; Jelks et al., 2008; Johnson et al., 2013; Richman et al., 2015; Warren and Burr, 1994). Freshwater mussels are a particularly vulnerable group that provides important water-filtration services (Layzer et al., 1993). In addition to being sessile, and therefore unable to move to avoid disturbance, many mussels depend on fishes to colonize new sites. As larvae (glochidia), they attach to the gills of a host fish, where they develop during transport to a new site. In rivers, upstream colonization is particularly important for these taxa (Terui et al., 2014). Lee and DeAngelis (1997) developed a structured model to study the spatial spread of mussel populations. The model showed that colonization patterns resembled a traveling wave front, with a faster velocity for mussel species maturing at an earlier age (Lee and DeAngelis, 1997). Understanding colonization rates is important to predicting recovery from disturbances, such as dredging, sedimentation, or chemical spills. In a subsequent paper, Lee et al. (1998) evaluated metapopulation dynamics of various Unionid mussels. A key result was that mussel species associated with a fish host having a restricted movement range require a high success rate of finding fish host to achieve at least an intermediate level of abundance. Mussel species with fish hosts having a limited range, coupled with a low success rate of finding a host, tend to be rare in numbers and sparsely distributed (Lee et al., 1998).

3.6 Research to understand the effects of river fragmentation and reconnection

IBMs have been used to understand the potential costs and benefits of reconnection options, including translocation and passage (Figure 6f). One result is that fish in upstream reaches are more likely to experience higher risk of extirpation than those in downstream reaches when barriers prevent upstream movement (Harvey and Railsback, 2012). An important finding is that export of larvae from short segments to downstream reaches can deplete upstream segments, a general result in physical systems where migration is asymmetric (Jager et al., 2001). These results emphasize the general idea that upstream recolonization is a fundamental problem for organisms in directional, advection-dominated systems.

A series of simulation experiments to compare reconnection options were conducted with an IBM of white sturgeon in the Middle Snake River. Translocation was found to be most successful when adults were transported upstream as far as possible to a reach with good habitat conditions (Jager, 2006b). In addition, a strategy of screening upstream reaches to prevent downstream movement was shown to be successful for simulated white sturgeon (Jager, 2006b). Conditions under which passage (Jager, 2006a) and translocation (Jager, 2006b) were beneficial depended on whether the recipient was upstream, having sufficiently large amount of habitat, and whether screening by trash racks to prevent large objects (including sturgeon) from entering turbine intakes was sufficiently narrow to prevent entrainment into turbines during downstream migration. Thus, mortality risk during migration through dams is an important consideration. In another study, a PVA model was used to evaluate the benefits of translocation for the humpback chub (*Gila cypha*) in the Colorado River, USA (Pine et al., 2013). The success of translocation depended on the relative survival in the donor and recipient reaches (Pine et al., 2013).

3.7 Research to understand genetics in riverine metapopulations

Simulating population and metapopulation (spawning populations linked by infrequent migration) genetics is an important reason for choosing to use IBMs (Figure 6g). Although substantial literature exists that uses non-IBM models, these typically require either an assumption of two important alleles or many alleles with small effects (i.e., statistical models that rely on a normal distribution of trait values). The earliest IBMs were more akin to genetic algorithms, motivated by the need to examine mutation effects (e.g., mutation meltdown) in small populations (Gabriel et al., 1993; Lynch et al., 1995). These models, used in conservation biology, focused strictly on neutral inheritance and not on selection resulting from decisions or activities of organisms.

The first genetic IBM (IBM+G) model was applied to the question of selection on fish size due to fishing (Martinez-Garmendia, 1998). In rivers, the first IBM+G quantified the effects of population isolation of white sturgeon between dams in the Snake River (Jager, 2001). These models simulated both selection and neutral genetics. They have many advantages over non-IBM population genetic models, including the flexibility to represent different genetic systems (e.g., polyploidy), intermediate numbers of alleles, interactions among loci, control genes, and effects of mating systems and other behaviors (e.g., homing migration) (Jager, 2001).

In many cases, IBM+Gs are used to understand the genetic effects of anthropogenic influences (e.g., harvest size selection, hatchery operation, fragmentation by dams, reconnection, climate change). Models of hatchery influences, for example, have shown that supplementation of lake sturgeon had little effect on allele retention and inbreeding (Schueller and Hayes, 2011). Modifying the numbers released to reduce selection was shown not to be effective. Once introduced to a growing population (such as one supported by supplementation), a few 'alien' alleles can quickly increase in frequency until they reach an equilibrium (Jager, 2005). Results from these IBM+Gs confirm that ensuring demographic health of populations often alleviates genetic concerns. Another purpose has been to explore the risk of hybridization, for example between pallid (*Scaphirhynchus alba*) and shovelnose sturgeon (*S. platorynchus*) (Jager unpublished data).

One exciting research direction is to understand how dendritic network properties influence riverine metapopulations. This has been explored using IBM+Gs (Labonne et al., 2008; Landguth et al., 2014). In one case, the combined effects of asymmetric dispersal along river networks, combined with overland movement (e.g., for amphibians or for fishes transported through floodplain inundation or being carried by non-aquatic organisms), was considered (Chaput-Bardy et al., 2009). The role played by traits that control homing behavior and spawning fidelity have not been fully explored. However, studies that simulate selection and genetic adaptation have been performed. These have shown that local adaptation can ‘rescue’ isolated populations in stream networks (Coombs et al., 2010; Letcher et al., 2007). Network properties were found to influence Chinook salmon growth in warmer thermal regimes (Fullerton et al., 2017). Juveniles in the least complex network grew faster and were ready to smolt earlier than those in more complex river networks (Fullerton et al., 2017). Other studies using IBM+G models to explore the ability of fishes to adapt to climate warming are discussed in the section below.

3.8 Research to understand the effects of warming and flow shifts under climate change

Modeling research using IBMs has addressed the potential effects of warming stream temperatures, as well as the effects of shifts in hydrology and timing of flows. A hypothesis has been that populations would shift toward cooler headwaters in response to warming, and concerns have been raised about barriers (e.g., dams) preventing such movements.

One study of potential effects of climate change evaluated interactions between shifts in flow (early snowmelt) and warming on a fall- and a spring-spawning trout (Jager et al., 1999) (Figure 6h). An unexpected result was earlier maturation of the spring spawning rainbow trout life history under warming. Similar results have been observed in currently forested streams where wildfire has removed canopy cover and warmed stream temperatures (Rosenberger et al., 2015). Simulating interactions between warming and changes in flow can produce complex effects. For example, brown trout, a fall spawning species, was not impacted as expected by scouring of redds (nests) when high flows shifted from spring to winter. Warming benefited both species in the upstream, but not the downstream reach. This supports the idea that climate warming will cause movement toward cooler headwaters (Jager et al., 1999). This result was also produced by a study of brook (*S. fontinalis*) and rainbow trout (*O. mykiss*) in the Appalachian Mountains, USA (Clark et al., 2001). More recently, an IBM+G developed from inSTREAM determined that declines in biomass and extinction risks were substantially larger under combined warming and flow reduction scenarios, despite stronger evolutionary responses (Ayllon et al., 2016). The traits that varied in this study were size at emergence and maturity size threshold (Ayllon et al., 2016).

Ultimately, it will be important to use IBM+Gs to address questions about adaptation to climate change. For example, climate adaptation via plasticity in growth has been explored for Atlantic salmon populations (Piou and Prevost, 2012, 2013). In another study, Anderson et al. (2013a) simulated phenotypic plasticity in adapting to shifts in seasonal events using an IBM. Model results suggested that population extinction can occur if the rate of change in the bioclimatic envelope exceeds the rate that the population’s phenology can change, or if the variability in the envelope exceeds the population's inherent capacity for withstanding climate variability. The perceptual abilities of individuals again play a role in framing the ability of populations to adapt. For example, a population with migration timing cued by photoperiod exhibited weaker phenotypic plasticity than one cued by temperature (Anderson et al., 2013a). Anderson et al. also found that a threshold leading to population extinction was foreshadowed by increased variability in average individual condition across years.

One concern is that climate change will have a ‘bottleneck’ effect on populations whereby decreased population size and the associated decrease in genetic diversity will prevent adaptation. A landscape-genetics IBM of bull trout (*Salvelinus confluentus*) model suggests that populations isolated by low flows under climate warming will face a risk of losing genetic diversity (Landguth et al., 2014).

Not all studies using IBMs to simulate population-level responses to climate change have predicted large effects. For example, Clark et al. (2001) found that species differences in fecundity explained their competitive outcomes better than the influence of climate. Another notable feature of that study was the use of a geographic information system to allow the model to be distributed across streams in a large region. More recently, an IBM was used to examine interactions between forest harvest and climate change in the Pacific Northwest, USA (Penaluna et al., 2015). Individual- and population-level responses were variable. In some cases, forest harvest countered the effect of climate change through increased summer flow. The most consistent response was earlier emergence of fry, but this change in timing did not necessarily result in population-level differences (Penaluna et al., 2015).

4. Where will the flow of ideas go next?

Dendritic networks, one-directional flows, and adaptations to predictable and unpredictable features of flow (and temperature) are defining characteristics of river habitats used by aquatic biota. Increasingly, questions about the viability of fish and mussel populations in river networks are being asked (Thomaz et al., 2016), and riverine IBMs are a logical tool to apply. Advances in network theory and modeling tools, used in conjunction with IBMs, can be used to understand basic questions, e.g., “How organisms maintain distributions in river networks?” and applied questions, e.g., “What is the optimal placement and management of dams?” Clearly, the mechanisms by which riverine metapopulations in dendritic, directional networks recolonize tributaries are fundamental to understanding river ecology and integrating network modeling frameworks with IBM+Gs will be required to address these questions.

The literature reviewed here reveals a strong bias toward IBMs describing fishes. Few examples exist of IBMs applied to aquatic species at risk other than fishes, suggesting an opportunity for future modeling research to rank threats and guide restoration efforts for mussels, gastropods, crayfishes, and other imperiled taxa (Jelks et al., 2008; Johnson et al., 2013; Richman et al., 2015). We see opportunities to help evaluate strategies for conserving non-fish imperiled taxa as well, and the ability to represent species interactions that may depend on species densities and individual encounters in flowing media (e.g., those between mussels broadcasting glochidia and their migrating fish hosts).

A strength of IBMs is the ability to simulate the decisions by individual organisms in response to the environment and each other. Capitalizing on this strength, we see considerable opportunity for implementing IBM algorithms for movement in robotic fishes used for research to understand the effects of hydropower and other industries that rely on rivers (Garcia-Magarino et al., 2017). By applying our knowledge about animal and group social behavior, motivation and responses to environmental fields, and our understanding of animal perceptual limitations and capabilities (which are often different from ours) (Pe'er and Kramer-Schadt, 2008), we see opportunities for advancement in this area.

On a related theme, integration between social agent-based models for human actors and IBMs for the riverine biota that are affected by their decisions is another frontier in applied research. Agent-based modeling has been used to allocate waste loads and water. Models fully integrating human decision makers with animals in downstream ecosystems have not been explored. We see this as part of a general trend toward integrating human and societal systems with ecological systems.

Finally, a frontier of research that remains is to integrate individual-based models with biogeochemical models and functionally-defined ecosystem states requiring mass balance (Grimm et al., 2017). This challenge is starting to be addressed by merging IBMs with dynamic ecosystem models (Strauss et al., 2017). The science to understand carbon and nutrient dynamics is increasingly focusing on the incidence of ‘hot spots and hot moments’ at the terrestrial-aquatic interface. Although biotic processes strongly mediate biogeochemical cycles at the terrestrial-aquatic interface, the challenge of developing hybrid models that combine these conceptually distinct approaches remains for our metaphorical ‘downstream’ researchers.

These are a few examples of many possible future directions, or unwinding braids, in the channel of riverine ecology aided by IBMs. Undoubtedly many others will emerge (Figure 1).

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6. List of Figures

Figure 1. Ideas originating in upstream tributaries merge at river confluences representing interactions among scientists bringing together ideas that influenced the development of river IBMs. Downstream, multiple channels represent downstream opportunities for future research. Motivating questions or topics are indicated by questions in italics and methodological influences and advances are in bold.

Figure 2. Schematic of a model for stream populations of fishes illustrating linkages between hysical Habitat Simulation (PHABSIM) as a function of flow and an individual-based model (IBM) of processes (reproduction, growth, movement, and mortality) that regulate each life stage. Population responses are illustrated for smallmouth bass, as simulated by (Jager et al., 1993).

Figure 3. Stommel diagram showing the range in spatial and temporal scales addressed by spatially explicit river IBMs. On the left, we indicate the reasons for adopting a spatially-explicit model and reasons for using an IBM.

Figure 4. Research questions addressed by riverine IBMs include those to understand a) population-level effects of flow regimes, b) species interactions, c) fish movement, and d) contaminant exposures. Other questions concern e) the conservation biology of imperiled riverine taxa including f) the effects of river fragmentation and reconnection, g) population-level genetic outcomes of management decisions, and h) future effects of global climate change.

Figure 1
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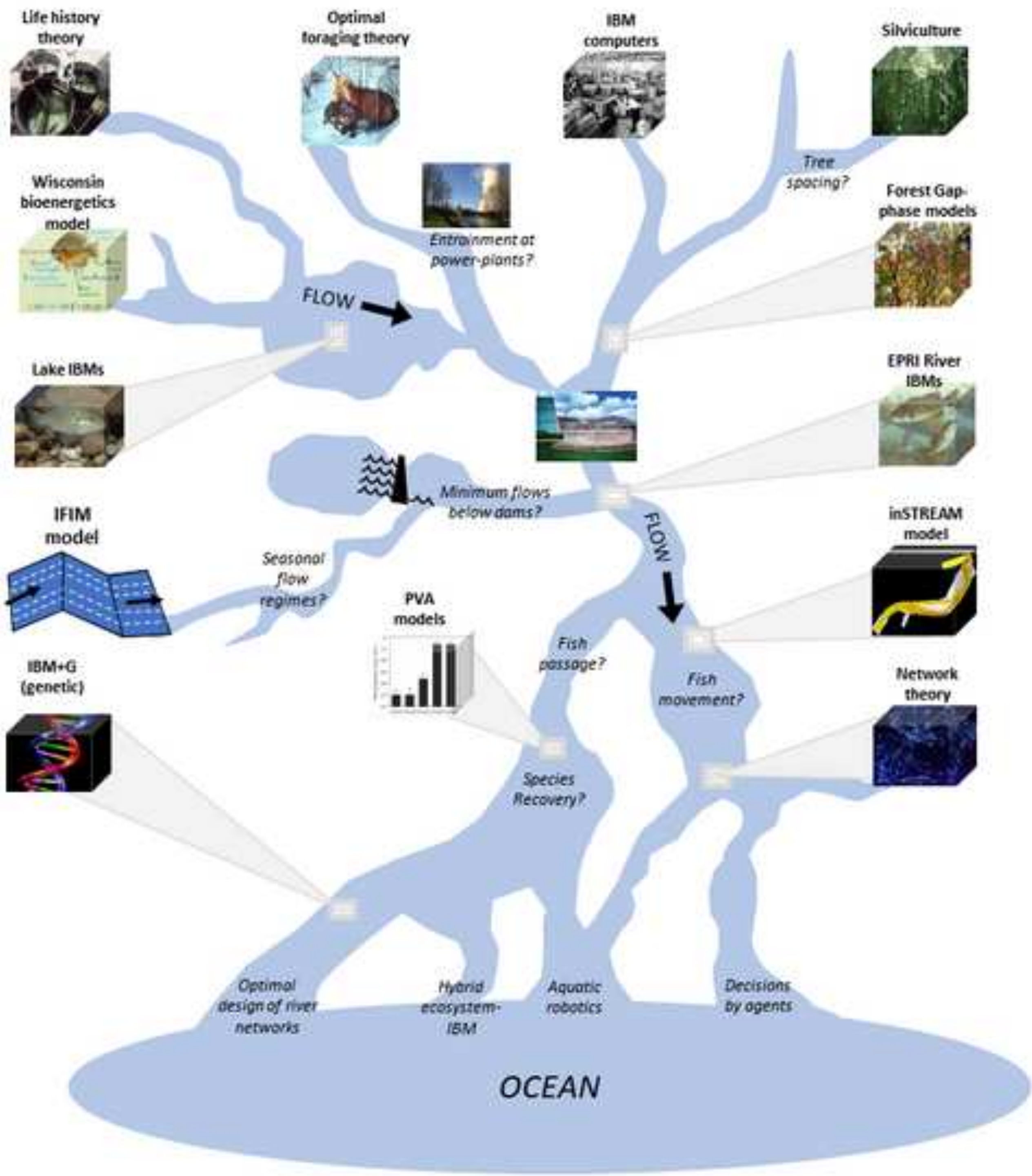

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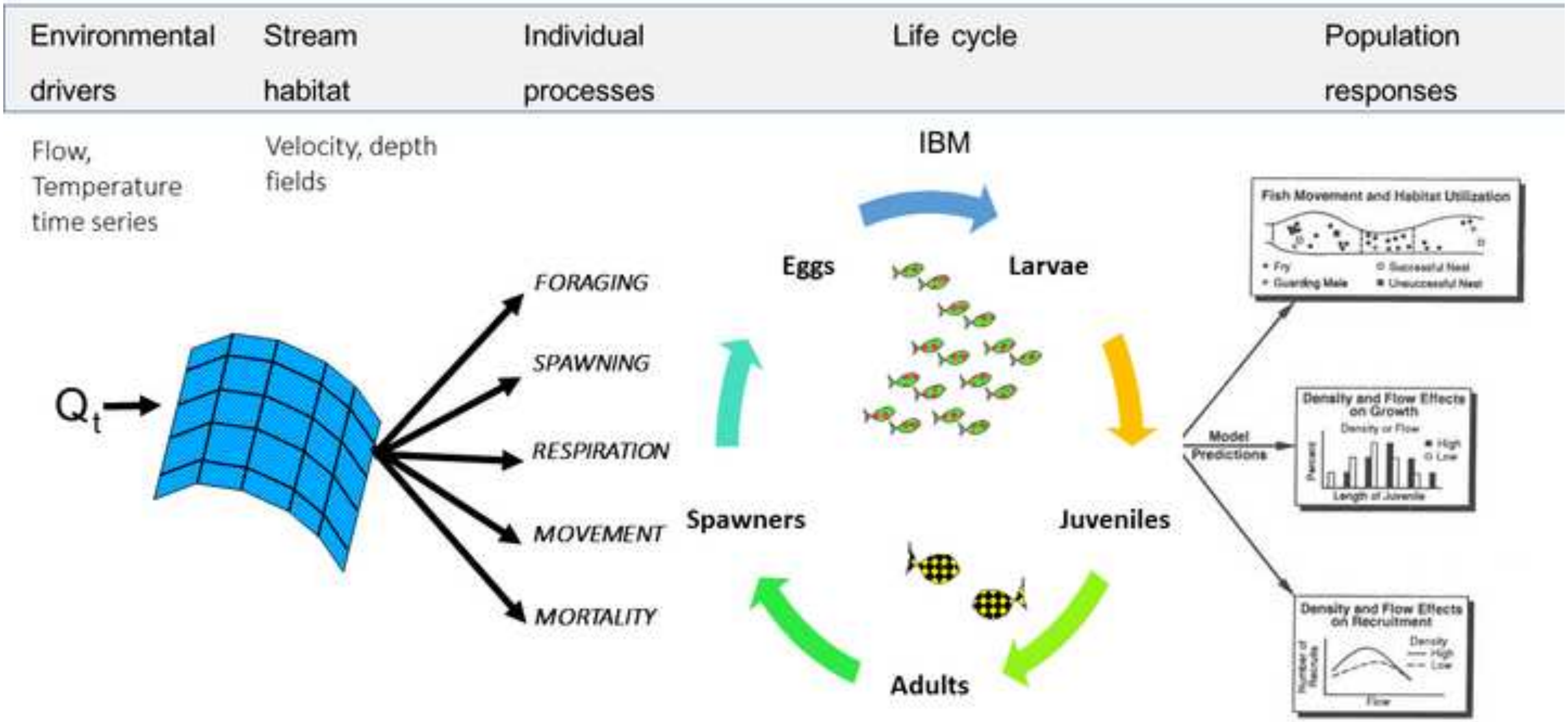

Figure 3

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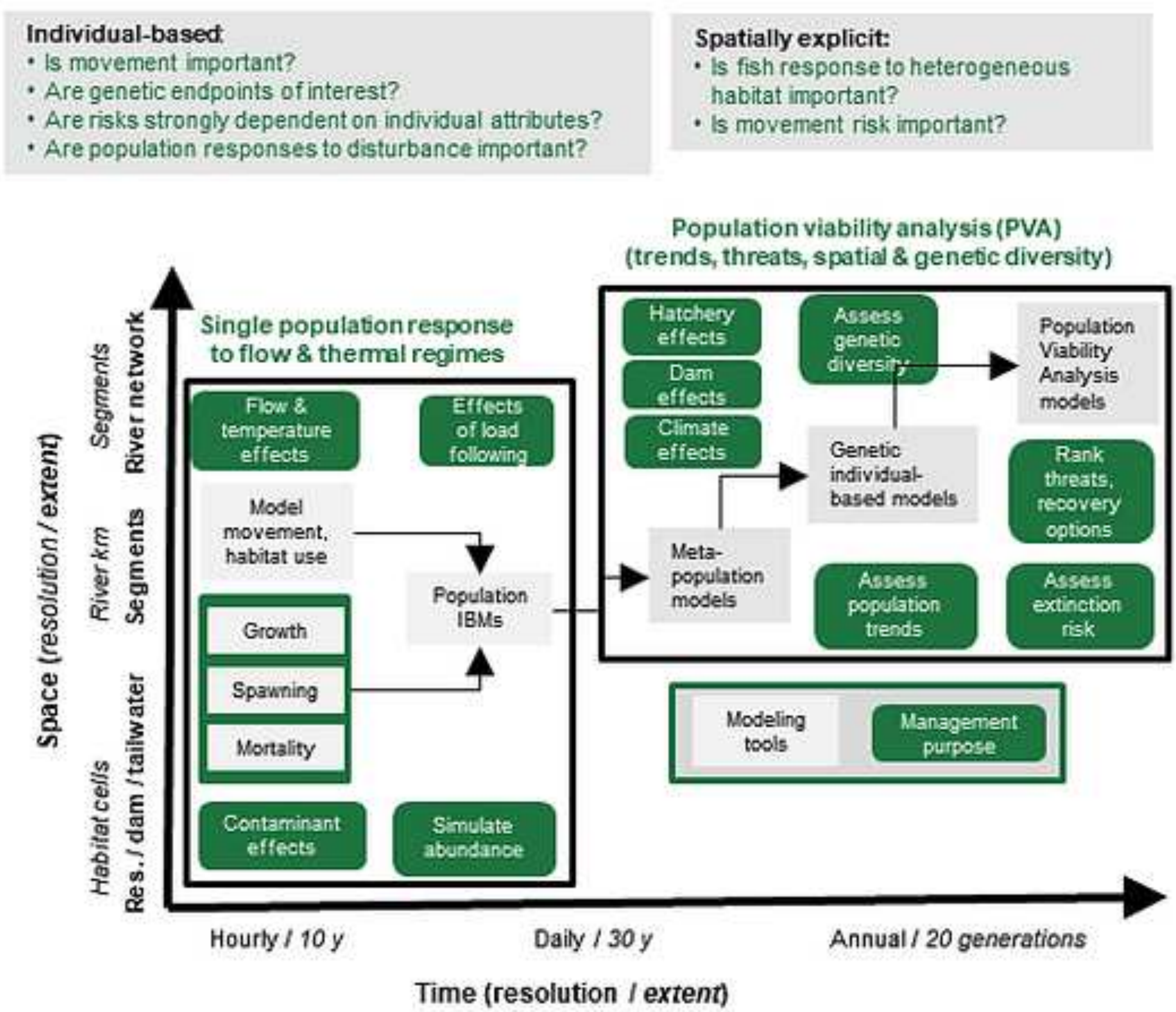

Figure 4
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