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Review

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

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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.

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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 (tributaries) 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 individual animals, 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 river fragmentation by dams 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, downstream channel that represents future river modeling research.

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 (Fig. 1). These downstream channels are different in size. A large productive inSTREAM modeling community of users is an important example. In addition, the initial Electric Power Research Institute (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.

The use of individual-based modeling in ecology, as depicted in Fig. 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 (Botkin et al. 1972) 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

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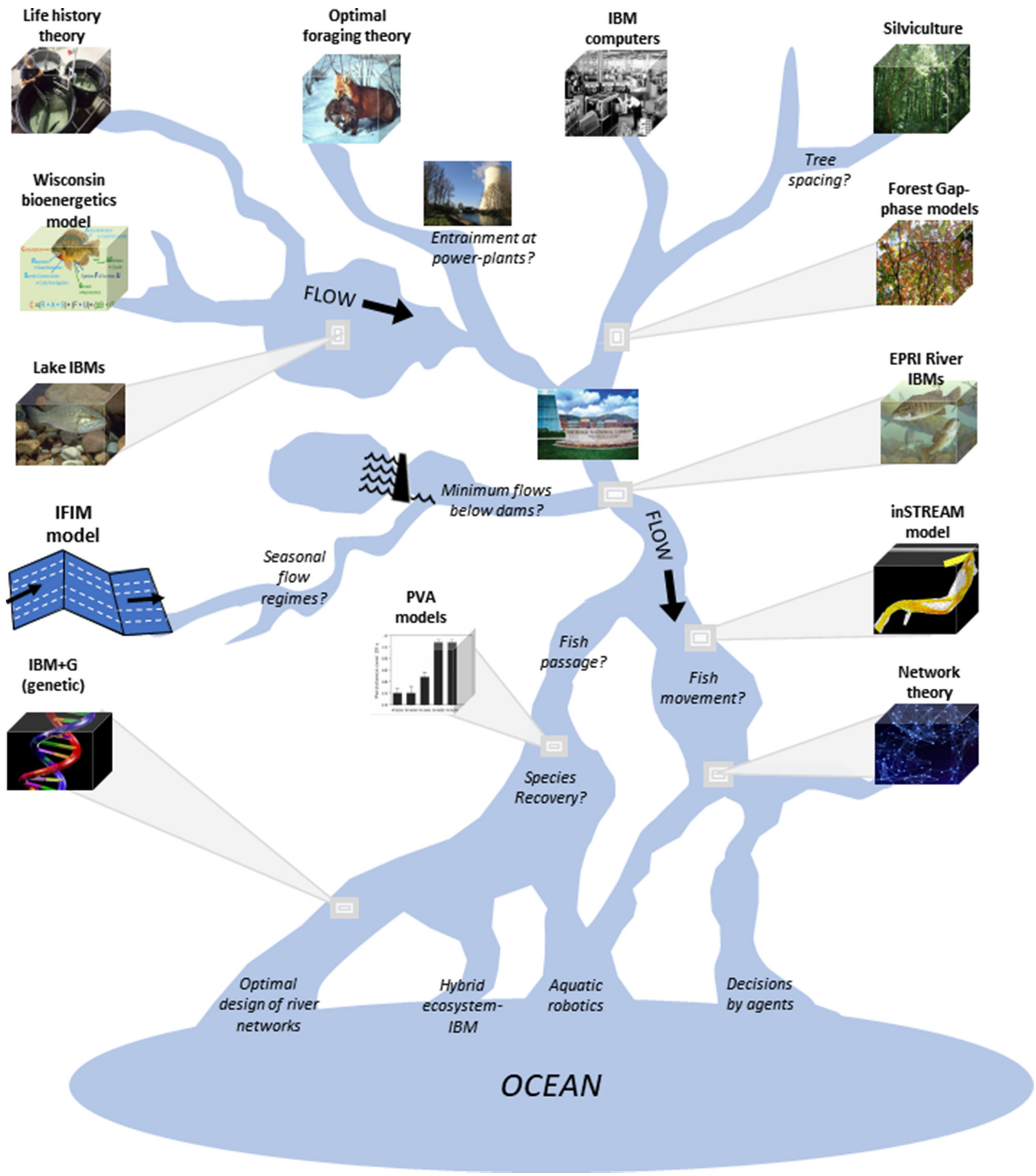

Fig. 1. Ideas originating in upstream tributaries merge at river confluences representing interactions among scientists bringing together ideas that influenced the development of riverine individual-based models (IBMs). Downstream, multiple channels represent downstream opportunities for future research. Motivating questions or topics are indicated by questions in italics and methodological influences and advances are in bold. Acronyms: Electric Power Research Institute (EPRI), Instream Flow Incrmeental Methodology (IFIM), and Population Viability Analysis (PVA), and International Business Machines (IBM).

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 young-of-the-year