

To appear in 6th International Conference on Hydroinformatics (2004)

**DECODING 3-D MOVEMENT PATTERNS OF FISH IN
RESPONSE TO HYDRODYNAMICS AND WATER QUALITY
FOR FORECAST SIMULATION**

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A theoretically- and computationally-robust mathematical approach for decoding movement patterns of individual fish responding to prevailing biotic and abiotic (physicochemical) stimuli is described. The modeling scheme, coupled Eulerian-Lagrangian agent- and individual-based modeling (CEL Agent IBM) is intuitive and based on well-established principles in computer science, fluid and water quality dynamics, computational fluid dynamics (CFD) modeling, neuroscience, and game and foraging theories. In short, a CEL Agent IBM couples a 3-D Lagrangian particle-tracker supplemented with behavioral rules into a Eulerian CFD model. Mathematical structure of the behavioral rules is derived from an agent-based, event-driven foraging model. Stimuli are queried from information provided by a CFD or water quality model or other a priori field data. CEL Agent IBM coefficients are biologically tractable. Back-casting simulation analysis results in a mechanistic mathematical formulation of behavior amendable to forecast simulation. In this paper, we describe the theoretical concepts of a CEL Agent IBM used to decode observed 3-D movement and passage patterns of downstream migrating juvenile salmon (migrants) at Lower Granite Dam on the Snake River, Washington, USA. The prototype CEL Agent IBM (the Numerical Fish Surrogate) is presently being used by the US Army Corps of Engineers to quantitatively evaluate plausible response of migrants to virtual designs of alternative bypass systems at federal hydropower dams before they are built. CEL Agent IBMs are applicable to many aquatic systems and provide the theoretical and computational facility for improving existing individual-based modeling and water resource decision-support.

INTRODUCTION

Understanding the spatial dynamics of aquatic populations and identifying factors contributing to movement behavior dynamics is critical to assessing and managing fisheries [Schmalz *et al.*, 1; Pelletier and Parma, 2] and for improving water resource management strategies [Van Winkle *et al.*, 3]. Understanding the movement of individuals is important because while individual movement can be translated into an understanding of population dynamics, the converse is generally not possible [Turchin, 4]. In many systems, the distribution of individuals is driven by environmental factors [Pientka and Parrish, 5] and should be evaluated prior to biological interactions [Hussko *et al.*, 6].

We introduce a mathematical method for decoding the movement behavior of individuals responding to prevailing biotic and abiotic (physicochemical) stimuli. The method is intuitive and based on well-established principles in computer science, fluid dynamics, computational fluid dynamics (CFD) modeling, neuroscience, and game and foraging theories. Mathematical formulations resulting from back-casting simulation analyses are mechanistic and amendable to forecast simulation. We discuss conceptual elements of the methodology employed to successfully decode 3-D movement patterns of downstream outmigrating juvenile salmon (migrants) observed at Lower Granite Dam on the Snake River, Washington, USA.

CEL AGENT IBMS

Complex simulation models are not new in ecology and have been criticized for three primary reasons: complex models are hard to develop, hard to communicate, and hard to understand [Grimm *et al.*, 7]. The best model is the one that captures features of interest with the fewest details [Haw, 8]. However, development of simple animal movement models is confounded by different theoretical approaches used in the analysis of animal movement and aggregation: Eulerian, Lagrangian, and discrete rules (agent-based) simulation [Parrish and Edelstein-Keshet, 9].

Model power and simplicity are achieved by coupling the theoretical treatments in a manner that maximizes the utility and minimizes the liability of each approach [Nestler *et al.*, 10]. Coupled Eulerian-Lagrangian agent- and individual-based modeling (CEL Agent IBM) integrates the approaches discussed in Parrish and Edelstein-Keshet [9]. In a CEL Agent IBM, a 3-D Lagrangian particle-tracking algorithm is supplemented with behavioral rules from an agent-based, event-driven foraging model [Anderson, 11]. The movement decisions of an individual are viewed as a balance of attractions to and repulsions from various sources or foci [Okubo, 12; Parrish and Turchin, 13] using concepts derived from game theory and computer science [Anderson, 11]. Three-dimensional movement behavior is implemented in a 3-D CFD model, U2RANS [Lai *et al.*, 14; 15], to take advantage of state-of-the-art numerical modeling of physicochemical fields in aquatic systems.

The focal point of simulation and analysis is the individual. Hypothetical swim path selection behaviors are explored using the virtual organism as a surrogate for the real organism. The specific goal is to uncover rules that embody the primary components of the strategy an individual of a target species, size, age, and life-stage uses to make movement decisions. In the full spectrum of prevailing physical, chemical, and biotic conditions, individual behavior is likely mediated by a synergy of diverse sensory inputs with various stimuli evoking conflicts in habitat preference. An individual, therefore, is unlikely to find a location that matches its preference on all environmental gradients, resulting in a hierarchy of responses to different cues which take varying precedence during the changing phases of a behavioral sequence [New *et al.*, 16; Sogard and Olla, 17].

Behavioral Rules

Behavioral rules governing the orientation and speed of individual movement are typically based on some measure of how an individual's fitness is expected to vary among alternative locations, under the assumption that animals make movement decisions at least in part to increase their fitness [Railsback *et al.*, 18]. Optimal foraging theory states that animals forage in ways that maximize energy input and minimize energy loss, which in turn influences movement patterns [Nowak and Quinn, 19]. Efficient foraging in a spatially and temporally heterogeneous environment requires that individuals be capable of acquiring and integrating different sources of information from within their environment [Hirvonen *et al.*, 20].

Agents

Object-orientation, or “agents”, provides a means of representation and formalism for representing the world in a manner that closely corresponds to animal perceptions [Bian, 21]. Multi-agent systems are powerful and flexible because the computer script is no longer centralized, but distributed in a multitude of autonomous agents. One can, therefore, add, eliminate, or modify agents without affecting the rest of the model [Ginot *et al.*, 22]. This results in a computer programming scheme that is both theoretically advantageous and one that is more efficient to create, evaluate, and modify compared to conventional techniques [Ginot *et al.*, 22].

Behavioral rules are derived from the agent-based, event-driven foraging model developed by Anderson [11]. Anderson's [11] foraging model melds classical approaches of game theory with precepts from neurobiology and bioenergetics. The model assumes that animals are rational operators that assess the opportunities and conditions of the environment and select behaviors that optimize their fitness. The animal's environment is described in terms of agents representing hydrodynamic, water quality, and biotic attributes (Figure 1).

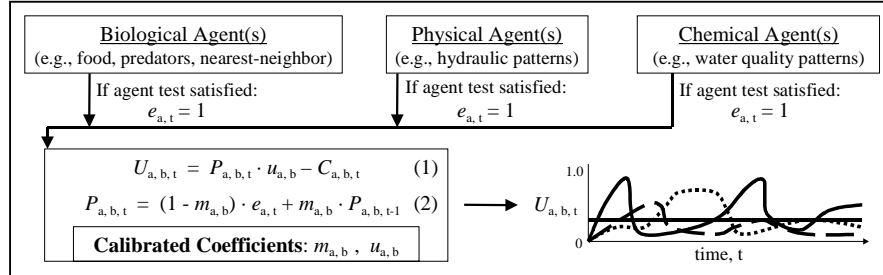


Figure 1. Relationship between agents, events, and behaviors in a CEL Agent IBM.

Events

Encounters between an individual and an agent in an increment of time are termed “events” [Anderson, 11]. Interaction between an individual and its environment usually involves the individual evaluating agent attributes at its location and in the surrounding vicinity followed by a movement response [Bian, 21]. Two modes of behavior may be associated with each agent. Tactical behaviors alter the outcomes of events (i.e., encounters with an agent) and strategic behaviors alter the probability of future events.

The manner of constituting an “agent variable” to quantitatively describe the attributes of an agent need not be uniform and may include additive, multiplicative, or some other combination [Anderson, 11] of variables. Events are usually associated with a change in the attributes of an agent [Bian, 21] as sensed by the individual. The probability an individual will respond to an agent increases as the agent variable increasingly exceeds a threshold value [Workman *et al.*, 23]. Event thresholds are not necessarily fixed and could be modified by experience [Anderson, 11].

Response

In each increment of time (t), using the cues on the presence or absence of an agent (a) characterized by stimuli (agent variables) being above or below threshold levels, the fish tracks the expected utility (U) of each behavior (b), tactical and/or strategic, and elicits the agent behavior response with the maximum expected utility. Based in game theory the expected utility from a behavior response to an agent in a given increment of time ($U_{a,b,t}$) depends on the behavior’s maximum or intrinsic utility (u) times the probability (P) of obtaining the utility, minus the bioenergetic cost (C) of the behavior, as in Eq. (1). The probability of obtaining the utility depends on the previous probability (P_{t-1}) and whether or not the individual encounters the agent in time increment t , as in Eq. (2). m is a memory coefficient weighting the present event and past probability. e is a Boolean measure equal to unity if the stimulus threshold is exceeded in an increment of time (i.e., an event for a given agent has occurred) and zero otherwise.

APPLICATION

A prototype CEL Agent IBM, the Numerical Fish Surrogate, was developed to decode observed migrant movement and passage patterns at Lower Granite Dam. More specifically, the objective was to demonstrate the utility of the Numerical Fish Surrogate in developing a theoretically-robust hypothesis explaining the swim path selection behavior of migrants. The Numerical Fish Surrogate and accompanying mechanistic behavior hypothesis would then be validated and, if successful, used to forecast plausible responses of migrants to virtual designs of fish bypass systems before they are built.

At Lower Granite Dam (Figure 2), the bypass system and other structural components known to influence migrant movement and passage include: a behavioral guidance steel curtain structure (BGS), a surface bypass collector (SBC), a trash boom, and a removable spillway weir (RSW, not pictured). The BGS and trash boom were present for both year 2000 and 2002 studies. The SBC was operated in year 2000 and the RSW in 2002. In 2002, the SBC was partially removed and not operated. Both the SBC and RSW passed collected fish into the spillbay nearest the powerhouse.

Three-dimensional information on the movement of individual fish (hatchery steelhead) was obtained through the use of acoustic-tags [Cash *et al.*, 24]. Run-at-large (i.e., non-species-specific) fish passage data was collected using fixed location multi-beam hydroacoustics placed at each passage route [Anglea *et al.*, 25; 26]. Acoustic-tag (AT) telemetry, hydroacoustic (HA) passage, and CFD modeled flow data were divided into independent data sets for simulation analysis. One of the year 2000 data sets were used to refine and calibrate the behavior algorithm and the remaining three 2000 data sets and the seven 2002 data sets were used strictly to validate the behavior hypothesis and Numerical Fish Surrogate percent passage forecasts.

Agents, agent variables, and events were preliminarily identified from a synthesis of existing peer-reviewed literature on fish mechanosensory system biology [Goodwin, 27]. Plausible swim path selection behaviors were then translated into mechanistic, rule-based behavior hypothesis algorithms using the event-based approach and evaluated using the Numerical Fish Surrogate. The resulting behavior hypothesis, the Strain-Velocity-Pressure (SVP) hypothesis, agents, agent variables, events, and mathematical details of the behavior algorithm are described in detail in Goodwin [27].

Results

Virtual fish (Figure 2) consistently respond to hydraulic structures in ways similar to monitored fish, and both were substantially different from the flow field. For example, the CFD model indicates that flow approaches the dam at a 60° angle and passes under the BGS. In both virtual and observed nighttime movement, fish divert from the flow and shadow the BGS. In the daytime, both virtual and observed fish mill in front of the SBC with some swimming back and forth between the SBC and a portion of the trash boom upstream from the attachment point to the spillway. These similarities are noteworthy because fish must resist the flow and execute consistent volitional

movements to maintain their positions. Concurrence between observed and virtual distributions is a strong test of a model [Bart, 28], especially when r^2 exceeds 0.65 [Prairie, 29]. A regression of observed and virtual passage estimates (grouped as turbine, spillway, or bypass passage) for all 11 independent cases against a 45° line indicating optimal fit yields an r^2 of 0.74 despite observational and process errors and inherent, natural variation in animal behavior.

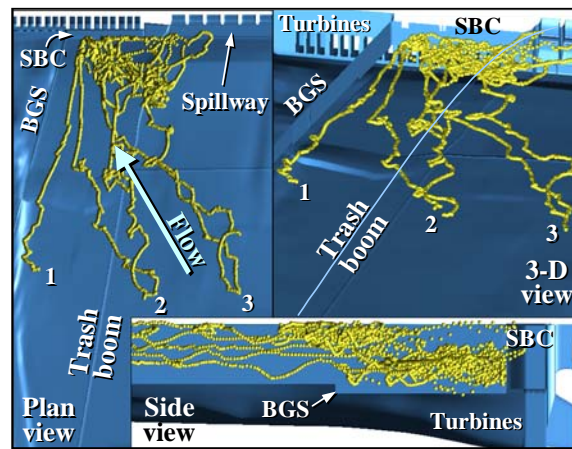


Figure 2. Movement of five virtual fish released at three subsurface (nighttime) locations {1,2,3} and two surface (daytime) locations {2,3}.

CONCLUSION

We demonstrate that models based on first principles from multiple disciplines can be linked together as simulation and forecasting tools and used to formalize and solve difficult environment problems. In our example, the Numerical Fish Surrogate simulated fish movements at a level of accuracy and resolution sufficient to guide engineering design of bypass structures.

ACKNOWLEDGMENTS

Tests described and the resulting data presented herein, unless otherwise noted, were obtained from research conducted under the sponsorship of the US Army Engineer District Walla Walla by the Engineer Research and Development Center. Permission was granted by the Chief of Engineers to publish this information.

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