SIMULATING MOBILE POPULATIONS IN AQUATIC ECOSYSTEMS

A Thesis

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Masters of Science

by

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ABSTRACT

Current spatiotemporal modeling techniques used to understand and predict ecosystem processes can often be categorized into one of two distinct modeling frameworks. Eulerian frameworks are often used to balance changes and fluxes of mass and energy and usually used in the simulation of physicochemical regimes. Lagrangian frameworks are often used to simulate the movement and/or behavior of individuals, groups of individuals, or populations. The use of different frameworks has created a disconnect between the modeling capabilities of physiochemical modelers (usually engineers) and biological population modelers (usually biologists). I describe a modeling framework, the Coupled Eulerian-Lagrangian Hybrid (CEL Hybrid) Ecological Modeling System, which couples the two frameworks into a comprehensive, unified framework for simulation of ecological processes. The CEL Hybrid modeling framework provides the means to simulate the spatiotemporal population processes, particularly movement dynamics, of higher trophic level species in aquatic environments.

The couple, the Numerical Fish Surrogate, allows movement behavior and other biological dynamics best simulated with a Lagrangian framework to be incorporated into Eulerian-based physicochemical simulation models. The Numerical Fish Surrogate (NFS) is, at its core, a particle-tracking algorithm enhanced with behavioral, or stimuli-response, rules. The NFS is the translation

mechanism that mediates between sensory inputs from the physicochemical environment and emergent behavior. To demonstrate the capabilities and potential of CEL Hybrid modeling, I developed and applied a CEL Hybrid Ecological Model to simulate the movement behavior dynamics of a cool water fish species, blueback herring (*Alosa aestivalis*), in J. Strom Thurmond Lake, a stratified southeastern impoundment.

Analysis of the results indicates the CEL Hybrid model performed well in reproducing the distribution of blueback herring in the reservoir for days when field data existed. Virtual sampling is introduced and used as the means to compare model output with actual field data. Comparison of virtual and actual fish distributions, as obtained from virtual and actual hydroacoustic surveys, in the vertical direction yielded an r-squared value of 0.93 while comparison of virtual and actual distributions along the longitudinal axis of the reservoir yielded an r-squared value of 0.67. I believe the results are good given the assumptions made and the inevitable shortcomings associated with development of a prototype.

BIOGRAPHICAL SKETCH

Richard Andrew Goodwin obtained an undergraduate degree in Civil Engineering, summa cum laude, from Virginia Polytechnic Institute and State University in 1996. In August 1996, Mr. Goodwin started graduate work at Cornell University, and in May 1998 began an internship with the Water Quality and Contaminant Modeling Branch at the U.S. Army Engineer Engineering Research and Development Center Waterways Experiment Station in Vicksburg, MS.

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Simulating Mobile Populations in Aquatic Ecosystems Using a CEL Hybrid Ecological Model: Concept Development

1.1 Abstract

Current spatiotemporal modeling techniques used to simulate and predict ecological processes may often be categorized into one of two distinct modeling frameworks. Eulerian frameworks are used to balance fluxes and changes of mass and energy and are usually used in the simulation of physicochemical processes. Lagrangian frameworks, on the other hand, are often used to simulate the movement and/or behavior of individuals, groups of individuals, and/or populations. I describe a modeling framework, the Coupled Eulerian-Lagrangian Hybrid (CEL Hybrid) Ecological Modeling System, which couples the two frameworks into a comprehensive, unified framework for the simulation of ecological processes.

In the coupled system, physicochemical regimes are simulated using a Eulerian framework, as before. Within the Eulerian-based structured environment, individuals or aggregates of individuals of a population move in response to simulated physicochemical conditions using stimuli-response rules. The rules are embedded in an 'enhanced' particle-tracking algorithm, creating the Numerical Individual Surrogate, or NIS. The NIS is then able to describe movement behavior and other selected processes that are best simulated using a Lagrangian framework. The NIS records the position, size, biomass, and age of each 'particle' and other relevant

parameters so that particles can be aggregated, converted, and integrated, if needed, into the same spatial averaging scheme used in Eulerian-based physicochemical regime simulations. The NIS allows the computer simulation to alternate between the Eulerian and Lagrangian modeling frameworks depending upon the needs of the simulation. The unified framework provides a platform for improved simulation of ecosystem processes because modelers can simultaneously exploit the advantages and strengths of each modeling framework.

1.2 **Introduction**

Scientists as well as policy-makers are increasingly aware that many of the values and services provided by healthy ecosystems cannot be adequately assessed by simply examining limited attributes of the physicochemical environment or by restricting evaluations of impacts to a limited number of living resource categories. Ecosystems have emergent properties only describable when the system is considered in its entirety. That is, the interplay between variables that results in observed ecosystem structure and function cannot be described when only a limited subset of the ecosystem is analyzed.

Full ecosystem-level analyses that realistically capture the dynamics of multiple hierarchical levels are rarely performed. Presently, the assessment of landscape and waterscape activities is typically constrained to a limited spatial scale, analyze a limited

number of processes, and/or analyze the dynamics of only a limited number of living resources. In many cases, however, the physicochemical environment of an ecosystem cannot be adequately predicted and assessed without considering feedbacks from higher trophic levels (Schaus *et al.*, 1997). In fact, biomanipulation of fish stocks is even used as an in-situ restoration technique to promote zooplankton grazing, decrease algal standing stocks, and increase water clarity (Badgery *et al.*, 1994). Changes in the stoichiometry of nutrient cycling, whether due to the presence of biota or alterations in food web structure, have direct impacts on physicochemical environment (Schindler and Eby, 1997). Similarly, higher trophic levels cannot be adequately predicted and assessed without considering the feedbacks from physicochemical processes of the ecosystem (Michaletz, 1998).

Improved natural resource management, restoration planning, and impact assessment requires improved knowledge and understanding through research on the interactive relationships between bottom-up factors (e.g., nutrient concentrations), top-down factors (e.g., fish populations), and the physicochemical environment (e.g., Badgery *et al.*, 1994). Acquiring this knowledge and understanding, however, requires additional tools, as current modeling methods are hardly available or sufficient (Tischendorf, 1997; Parrish and Turchin, 1997).

Presently, multidimensional spatiotemporal analytical techniques used to simulate ecosystem processes (e.g.,

physicochemical environment, lower trophic levels, higher trophic levels, etc.) can be classified as belonging to one of two analytical approaches, or analytical frameworks: Lagrangian or Eulerian (Turchin, 1997). Each analytical framework has unique capabilities and liabilities, and neither framework is able to capture all the spatiotemporal dynamics of an ecosystem. In this chapter, however, I describe an approach for using an existing numerical modeling technique to integrate both frameworks into a single, unified analytical approach, or framework, that I believe is capable of capturing many, if not most, dynamic mechanisms that constitute an ecosystem. This technique, the Coupled Eulerian-Lagrangian Hybrid (CEL Hybrid) Ecological Modeling System, provides the foundation needed for improved simulation of ecosystem processes because modelers can avoid many of the liabilities and simultaneously exploit the strengths of each distinctive framework.

1.2.1 **Traditional Modeling Approaches**

The models employed by biologists and engineers to simulate various components of the same ecosystem often differ in the modeling framework used. This creates a disconnect between the modeling capabilities of biologists and engineers. Models used by biologists to simulate the movement behavior of organisms are often Lagrangian-based, that is, they are centered on the individual (e.g., Parrish and Turchin, 1997). Individual movement may then be characterized by a position, a velocity, and even an acceleration

(Turchin, 1997). On the other hand, models used by engineers to simulate physicochemical regimes are almost always Eulerian-based, that is, they are centered on a point fixed in space. Fluxes of mass and energy can then be routed through the system, represented mathematically as a series of interconnected compartments fixed in space, and balanced at compartment interfaces using established equations (Thomann and Mueller, 1987).

1.2.1.1 *Simulation of Animal Movement*

Although animal movement can be modeled using the Eulerian framework, by representing the movement of individuals as fluxes and/or diffusions of population densities (e.g., Okubo, 1980; Edelstein-Keshet, 1988; Turchin and Simmons, 1997), the Lagrangian framework is preferred since a detailed understanding of individual movement can be translated into an understanding of population redistribution, while the converse is generally not possible (Turchin, 1997). In addition, the use of individual positions and vectors enhances the compatibility with tracking data and analytical treatments of movement processes (Tischendorf, 1997).

1.2.1.2 *Simulation of Physicochemical Regimes*

Although the Lagrangian framework is used, at times, in physicochemical modeling, e.g., to decouple advection from diffusion in hydraulic modeling (Oliveira and Baptista, 1995), the simulation

of physicochemical regimes requires the use of a Eulerian framework (a structure fixed in space) to route and balance mass and energy fluxes. In order to use many established flow and chemical equations, these mass- and energy-balance models must represent a system, mathematically, as a series of interconnected compartments, within which physicochemical conditions are averaged. Mass and energy may then be routed through compartments and balanced at compartment interfaces. Compartments may be one-dimensional (i.e., a line segment), two-dimensional (i.e., a grid cell), or three-dimensional (i.e., a box, pyramid, etc.). After accounting for sources and sinks of mass and energy within and bordering the system, a virtual representation of the flow and water quality regimes within an aquatic system, for instance, can be generated. In addition to physicochemical simulations, the Eulerian framework has proven useful for modeling dynamic processes of lower trophic levels (e.g., Gin *et al.*, 1998). As with physicochemical simulations, however, spatial and temporal resolutions must be adequate to capture essential processes and dynamics.

1.2.1.3 *Disconnect Between Modeling Frameworks*

The different numerical approaches used in Lagrangian and Eulerian schemes provide each framework with unique attributes (Figures 1.1 and 1.2). These unique attributes translate into unique capabilities and liabilities associated with each framework. For

instance, transport equations are often solved in Lagrangian form, particularly when simulating animal movement, because the Lagrangian form of such equations is often simpler to understand, visualize, and implement. At the same time, however, Eulerian schemes may sometimes be preferred to avoid the lack of formal conservation from which Lagrangian schemes suffer (Gravel and Staniforth, 1994). This may be particularly important, for instance, in simulating the fate and transport of bacteria where tracking the movement of individual particles and ensuring conservation (i.e., accounting for the addition, loss, and change in mass and form of all individuals) may prove difficult and/or computationally demanding. For such simulations, modeling concentrations or densities may prove more convenient and equally viable. In Lagrangian schemes, conservation has to be imposed as an additional constraint on the system.

Lagrangian schemes often offer the ability to use larger time steps than Eulerian-based models, with no loss of accuracy. This may be an attractive property, for instance, when simulating a species' annual reproductive cycle since a Eulerian-based model may require shorter time steps, therefore, increasing the computational resources needed. Eulerian-based simulations often require the use of shorter time steps to maintain computational stability (Gravel and Staniforth, 1994).

- Focused on the Individual
- Continuous Spatial Information
- Longer Time Steps Possible
- Preferred for Simulating Animal Movement

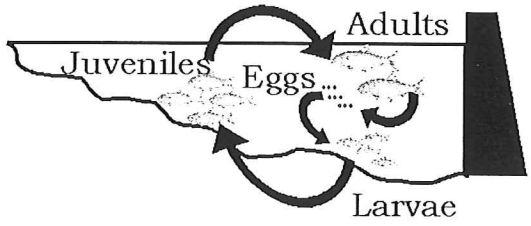

Figure 1.1 Attributes of Lagrangian-based numerical schemes.

- Based on Coordinates Fixed in Space
- Discontinuous Spatial Information (Information Averaged by Compartment)
- Shorter Time Steps Often Needed
- Often Convenient to Solve Physicochemical Equations

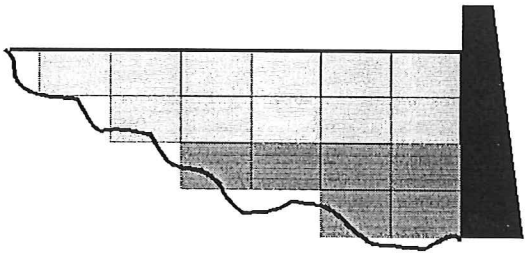

Figure 1.2 Attributes of Eulerian-based numerical schemes.

The liabilities of each framework, particularly the Eulerian framework, are often disregarded. For instance, population processes best simulated in Lagrangian form (e.g., movement of individuals) are often forced into Eulerian-based models (e.g., physicochemical models) by converting the individuals into biomass, or other such Eulerian-based quantities. Consequently, population processes must then be described in terms of the biomass in each compartment (e.g., grams of carbon per unit volume), as opposed to a tally of individuals. Similarly, changes in the population are simulated as mass fluxes, as opposed to an increase or decrease in the number of individuals. Capturing the population dynamics of a species in such a reference frame is difficult because population dynamics are often based on the behavior of individuals, or groups of individuals, and not on spatially-integrated averages (Figure 1.3). Individuals that contribute to inter-population and intra-population processes are not evenly distributed in time or space and, therefore, cannot be realistically averaged for placement into a Eulerian framework. Similar kinds of averaging errors occur when members of many different species, each with specific relationships to the rest of the ecosystem, are lumped into a relatively few trophic levels, obfuscating the response of species, life stages, or individuals to changing environmental conditions. In addition, the structuring factors in food web organization may not be clear (Murtaugh and Kollath, 1997) making it difficult to assign species in a food web to trophic levels.

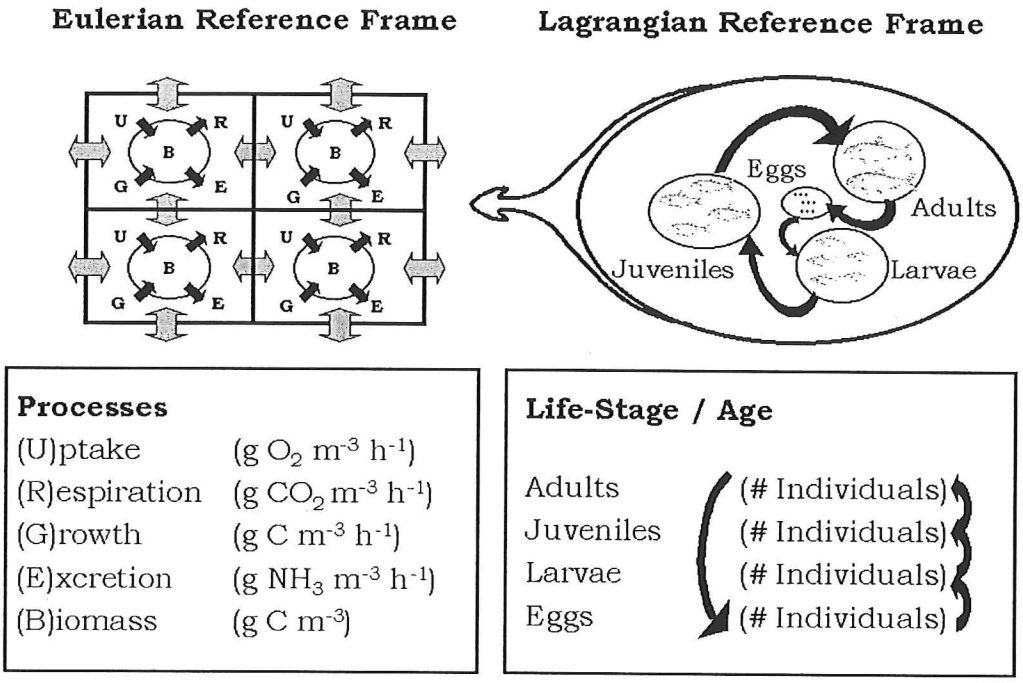

Figure 1.3 Integration of population dynamics into a Eulerian framework.

While some organisms (e.g., zooplankton, phytoplankton, bacteria, etc.) may be best simulated as Eulerian-based quantities (e.g., concentration or density of individuals in each compartment), the simulation of many biological organisms would benefit from decoupling those attributes best simulated in a Eulerian framework from those best simulated in a Lagrangian framework, and at the same time maintain the integrity of the simulated organism. The simulation of highly mobile higher-trophic level organisms, in particular, would benefit from such treatment since their complex movements are difficult to capture in a Eulerian framework

(Breitburg *et al.*, 1997). At the same time, however, their influence on local physicochemical conditions, e.g., local water quality, due to respiration, excretion, and other processes must be modeled in a Eulerian framework (i.e., integrated into Eulerian-formulated physicochemical equations). Consequently, a modeling framework hoping to capture the full suite of dynamics and processes constituting an ecosystem cannot restrict its perspective to either a Eulerian or Lagrangian framework. Realistic simulation of complex ecosystem processes requires the use of both modeling frameworks.

1.3 **Foundation and Description: CEL Hybrid Ecological Models**

1.3.1 **Coupling Eulerian and Lagrangian Frameworks**

Despite the differences between Lagrangian and Eulerian modeling attributes, these differences need not be an impediment to the development of advanced modeling capabilities. In fact, it is the differences between the two modeling frameworks that provide the opportunity for modeling abilities not yet realized. The key to establishing a new modeling paradigm for simulating a full range of ecosystem-level processes is to identify unifying concepts between the contrasting Eulerian and Lagrangian frameworks. The Lagrangian framework maintains the integrity of an object as it moves through simulated space (Figure 1.4) since the framework is centered on the individual. In contrast, the Eulerian framework is centered on a point fixed in space and, thus, cannot track the movement of individual objects. Instead, the Eulerian framework

requires that individual objects be converted into compartment-averaged values, e.g., concentrations or densities of individuals, which can then be transported through the system as a series of fluxes across compartment interfaces (Figure 1.5).

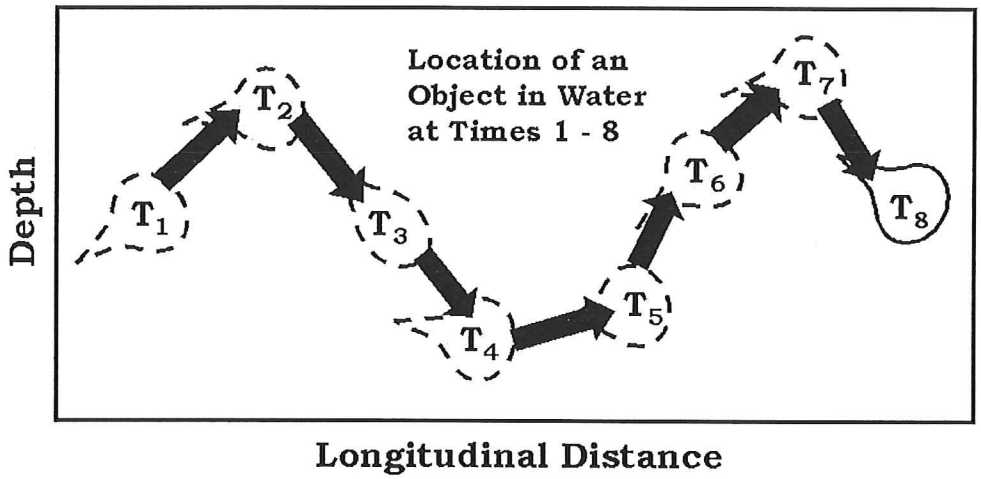

Figure 1.4 The Lagrangian modeling framework, in most computer models, can be described as analogous to a 'moving' frame of reference, which allows an observer to track the path of an object through space. The exact location of the object in space (x-, y-, z-coordinates) is known at each time step.

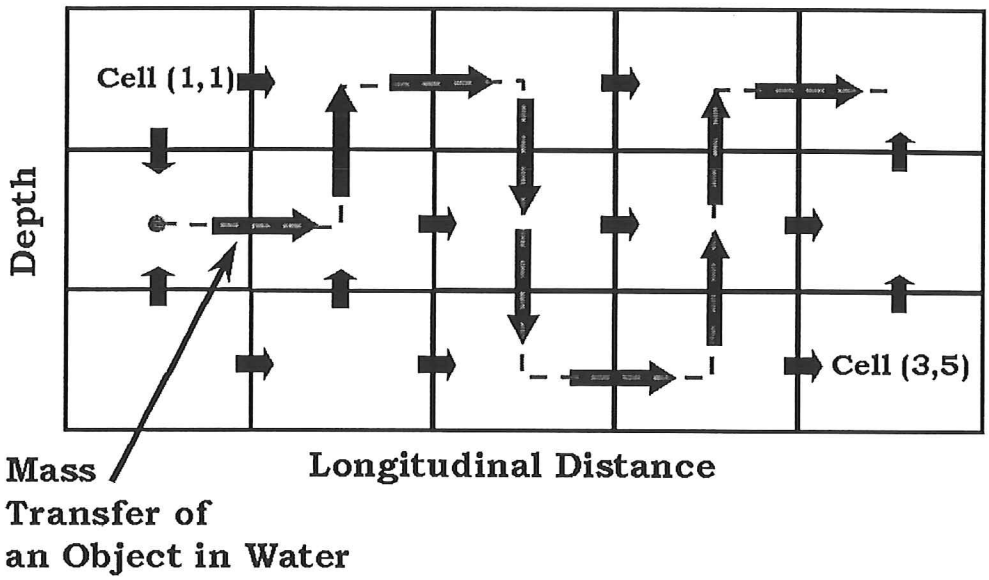

Figure 1.5 The Eulerian modeling framework uses a set of fixed points in space around which mass and momentum can be balanced. Without supplemental transport equations, the only way to transport an object in a Eulerian-structured environment is to convert it into a compartment-averaged value; the 'object' is then transported to other cells by way of fluxes across compartment interfaces. The object's exact location in space is not defined.

From the perspective of a Eulerian-structured environment, an individual organism in a Lagrangian-based model, where physicochemical processes/conditions are not simulated, may be viewed as a particle (i.e., a point in space) (Matuda *et al.,* 1993) implicitly positioned within one large compartment (i.e., an environment where all physicochemical conditions are uniform). If the particle represents an individual, or some aggregation of a

population (LePage and Cury, 1997; Rose *et al.*, 1996), then a particle-tracking algorithm can be employed to move the particle in response to physical forces (e.g., flow) and environmental conditions (e.g., water quality) computed by the Eulerian-based model as well as in response to the presence of other 'particles' (Matuda *et al.*, 1993; Parrish and Turchin, 1997).

1.3.2 **Particle-Tracking**

In aquatic systems, in particular, particle-tracking algorithms involve the use of discrete particles to model the transport and dispersion of a tracer or contaminant. They have been used extensively for decades to investigate sea ice transport, ocean fronts, oil spills, tidal-dispersion processes, chaotic stirring in tidal environments, and the fate of floatables and dissolved and suspended materials (Scott, 1997; Chapman *et al.*, 1994). For use in aquatic systems, a particle-tracking algorithm generally works by: 1) referencing hydraulic information at given locations in the Eulerian-structured system, 2) interpolating the hydraulic information to obtain the needed information at interior points within compartments, and 3) using the interpolated information as a surrogate for continuous spatial information that is then used to move an object in the compartments. Interpolation provides the means to generate a nearly continuous information field while at the same time allowing the information to change over time and space as simulated in the Eulerian-based physicochemical model.

1.3.2.1 *Enhanced Particle-Tracking with Behavioral Rules*

The ability to simulate dynamic spatial information fields and, at the same time, maintain the integrity of moving objects in continuous space allows for the behavior of individual organisms to be modeled, in a virtual ecosystem. For aquatic applications, the simulation of physicochemical regimes, in essence, creates a virtual aquatic environment in which individual organisms may be placed. Recognizing that movement decisions of an individual group member can be viewed as a balance of forces (Okubo, 1980), behavioral cues, or stimuli-response rules, can be programmed into a particle-tracking algorithm to emulate a species' movement behavior. In particular, these rules dictate the attractions to and repulsions from various sources or foci (Parrish and Turchin, 1997). Enhancement of the particle-tracking algorithm through the addition of stimuli-response rules, which when taken as a whole dictate the pattern of movement (Schilt and Norris, 1997), creates a virtual organism. This virtual organism is then capable of making individual movement decisions in a way that emulates the behavior of real organisms.

Niche theory is the basis upon which stimuli-response rules are developed. Niche theory tells us that species have ecological "preferences," meaning they are found in areas where environmental variables have some "optimal" value (Legendre *et al.*, 1997). Given this, virtual organisms can be created and programmed, for

instance, to avoid areas of low dissolved oxygen, high water temperatures, or significant toxic concentrations. Methods for acquiring the information needed to build such stimuli-response rules for aquatic species are discussed in Nestler and Goodwin (1999).

If the 'enhanced' particle-tracking algorithm is then combined with other models that capture aspects of a species' behavioral ecology (e.g., Nonacs *et al.*, 1994) and bioenergetics (e.g., Schindler and Eby, 1997; Stockwell and Johnson, 1997), the CEL Hybrid Ecological Model could be used to assess the effects of ecosystem-level changes on species populations as well as to feed back the responses of the species to local physicochemical processes. Rule-based models can provide useful input into the design of biodiversity management strategies because of their ability to assess the importance of different mechanisms (Skelly and Meir, 1997).

1.3.3 **The Duality of Organisms**

Depicting individuals of a population as particles recognizes the duality that large, mobile organisms exhibit. That is, they have some attributes that are best simulated using a Lagrangian framework and other attributes that are best simulated using a Eulerian framework. Attributes of the species population under study must be sorted into those that are best simulated using a Lagrangian framework and those best simulated using a Eulerian framework. For example, the Lagrangian framework may be

preferred for simulating processes and attributes such as mortality, recruitment into the adult population, and fecundity since these all have strong spatial ties. The Eulerian framework, on the other hand, is best suited for simulating biochemical and bioenergetic processes. Biochemical and bioenergetic processes such as respiration, excretion, and decomposition are best simulated using physicochemical equations most conveniently solved using the Eulerian framework.

Depicting an organism, or group of organisms, as a particle capable of moving continuously through simulated space is the conceptual building block for complex simulations of ecosystem-level processes. Development of the conceptual framework can be thought of as follows:

- A semi-permeable barrier is placed in a water body (Figure 1.6a) so the system is represented as two, nearly separate, entities (Figure 1.6b). Placement of the barrier could be arbitrary or coincide with characteristics of the water body such as a thermocline location. From the population modeling perspective, there are now two populations. Typically, this is referred to as a meta-population; each subpopulation is represented as a single 'particle'. From the Eulerian perspective, the water body is represented as two compartments, each having unique and uniform physicochemical conditions.

- Different physicochemical conditions are allowed to elicit differing behavior in the subpopulations, all else being equal.
- Migration between the subpopulations through the semi-permeable barrier is permitted (Figure 1.6c).

Numerous characteristics of the physicochemical environment may be used to elicit responses from an organism. In aquatic systems, for instance, characteristics may include, but are not limited to, water quality constituents such as temperature, nutrients, and toxics as well as hydraulic variables such as velocity, acceleration, turbulence, and pressure waves.

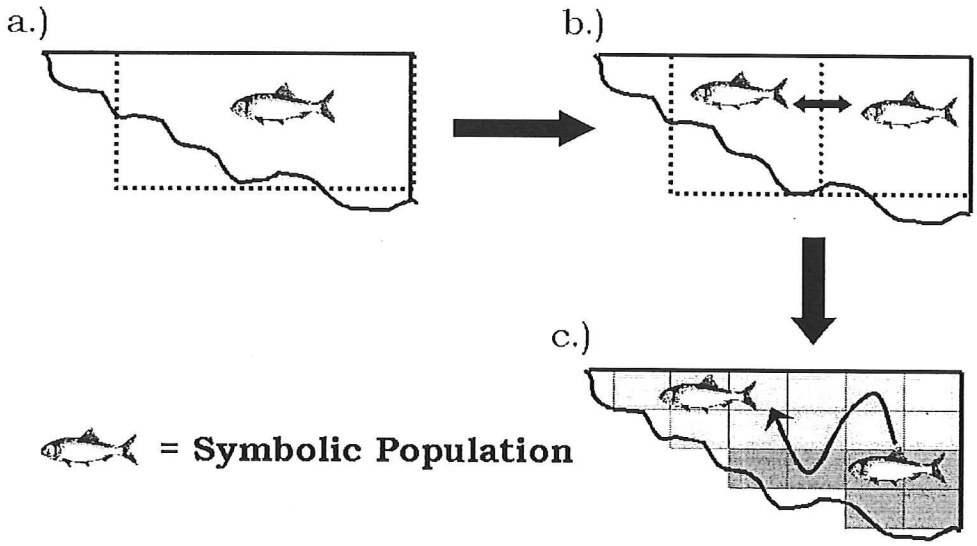

Figure 1.6 Strategy for spatially distributing a population in a Eulerian-structured aquatic system.

After redistribution of the particles (i.e., individuals of the subpopulations) in time, each portion of the population may

participate in selected biological processes such as death, birth, or recruitment into the next age/size stage. Physicochemical conditions, such as water quality or hydraulics, may influence these biological processes. Once the subpopulations have participated in selected biological processes, they can be categorized based on an appropriate criterion into stages (e.g., eggs, larvae, juveniles, and adults) or ages (e.g., 0-year olds, 1-year olds, 2-year olds, and 2+ year olds). Characteristics of the population relevant to physicochemical processes (e.g., number of individuals) can then be converted into Eulerian-based quantities (e.g., biomass, mass of nutrient generation, mass of nutrient uptake) using conversion factors so the influence of biological organisms, e.g., uptake, excretion, decomposition, etc., on the physicochemical environment can be accounted for.

With the conversion of selected population characteristics into Eulerian-based quantities, virtual organisms can influence physicochemical processes (e.g., Schindler and Eby, 1997) simulated by the Eulerian-based model. Accounting for such influences may prove important in achieving accurate simulation of ecosystem conditions. Fish schools, for instance, can alter dissolved respiratory gases (McFarland and Moss, 1967) as well as increase ammonium and nutrient concentrations (Oviatt *et al.*, 1972; Meyer *et al.*, 1983; Bray *et al.*, 1986). The modeling of such influences is not new. McFarland and Okubo (1997), for instance, modeled the oxygen consumption within a mullet school.

Using particles to represent organisms provides an added flexibility. Organisms can be aggregated differently to fit the scale of the analysis. For example, one particle may represent an entire population. Another alternative is to allow each particle to represent an individual organism or aggregates of individuals as is done in individually-based models (IBMs). Obviously, there is a gradient from which to choose the appropriate particle representation. Individual organisms can be aggregated in multiple ways. Each particle could represent from one to many individuals of equal size, age, sex, or life-stage depending upon the complexity of the problem, the speed of the computer, or other factors that might influence the level of aggregation necessary to address a particular issue.

1.3.4 **Markov Chain Behavioral Algorithms**

A key ingredient in implementing CEL Hybrid Ecological Models is the ability to develop algorithms capable of realistically simulating the movement behavior of large and/or abundant animals within ecosystems. This can be achieved through the use of discrete-time Markov Chains. Markov Chains are often used by animal behavioralists for describing the complex behavior of individual animals (Haccou and Meelis, 1992) and provide the most comprehensive foundation for simulating animal movement behavior.

A Markov Chain can represent a dynamic system consisting of several distinct, mutually exclusive states where specific probabilities exist for changing between states. In a behavioral system, a Markov Chain representation requires that an individual organism exist in one of a number of distinct, describable, and mutually exclusive behavioral states. For example, an organism may exist in one of three separate behavioral states: resting, feeding, or migrating. Unique probabilities are associated for changing between each state. The probability of moving from a "feeding state" to a "resting state", for example, may be 0.1 at each time step. For a given species and state of behavior, movement behavior rules can be developed to predict the movement of individual organisms.

An assortment of rules can be assembled to best simulate realistic movement. For example, a reasonable rule for emulating the movement behavior of salmon in a "migrating state" may be to have the particle, or virtual fish, swim at its physiological maximum swimming speed upstream against the flow, to have the virtual fish select the lateral location within the stream channel with minimal downstream water velocity, and to have the virtual fish swim at a depth having the least turbulence. Movement behavior rules may also be developed for daytime and nighttime behavior as well as spawning and non-spawning behavior.

The Markov Chain statistical model facilitates the simulation of complex movement behavior using states of behavior and allowing for the modification of species responses to physicochemical

conditions based on the current behavioral state. Different stimuli-response rules can be employed within each distinct behavioral state. Most long-term applications of Markov Chain statistical models, however, require substantial numbers of states since the response of an organism to stimuli may depend on the time of day, season of the year, life-stage, time since last feeding, or other factors, all of which must be represented as "states of behavior". In addition, state-specific population dispersion may be incorporated by allowing individuals to switch between different probability-based random movement processes depending on their behavioral state or other factors. The switching process itself could be modeled as a finite state Markov Chain (Blackwell, 1997).

1.4 **Qualities of CEL Hybrid Ecological Models**

The Coupled Eulerian-Lagrangian Hybrid (CEL Hybrid) Ecological Modeling System is a developed application of a Eulerian-Lagrangian method. Eulerian-Lagrangian methods (ELMs) have evolved over the last three decades to become one of the most attractive modeling techniques (Oliveira and Baptista, 1995) in numerous fields. Eulerian-Lagrangian concepts were introduced in the 1950's and 1960's and have been used to simulate everything from fluid flows (e.g., Udaykumar *et al.*, 1996) to the transport of material in fluids (e.g., Chapman *et al.*, 1994) to the dynamic behavior of leukocytes (e.g., Tran-Son-Tay *et al.*, 1998). However, a

literature search revealed that ELMs have not been widely applied in the field of ecological modeling.

Benefits of ELMs include, among others, the ability to decouple processes best simulated using a Lagrangian framework from those best simulated using a Eulerian framework (e.g., advection and diffusion processes in hydraulic modeling) and the potential for savings in computational resources resulting from the ability to use longer time steps, for certain processes, without loss of accuracy. For ecological modeling, mixed, or coupled, Eulerian-Lagrangian frameworks have improved capabilities over traditional Lagrangian-based population, or animal movement, models and Eulerian-based physicochemical models for the simulation of ecological processes.

1.4.1 **Improved Mathematical Accuracy**

Predictions made by mass-balance models may differ from predictions made by models that consider individual elements of a system, or small aggregations of elements (particularly, individual-based population models), in those situations where the interactions between individuals influence the outcome of a simulation. For instance, consider a hypothetical ecosystem comprised of 30 grid cells (Figure 1.7). The interactions between individuals of differing cells can be ignored if densities do not exhibit substantial temporal or spatial variability (Figure 1.7, Ecosystem 1) because the interactions can be treated as a constant within the analysis.

However, if densities do exhibit substantial temporal or spatial variability (Figure 1.7, Ecosystem 2), then the type or degree of interactions between individuals may also change substantially; a situation not easily handled by mass-balance models, but easily addressed by Lagrangian-based population models. As an example, in a lake setting, a mass-balance model may predict a transformation of prey fish biomass into predator fish biomass even under very low prey density. However, a model that considers the exact locations and interactions among individuals may show no transformation of prey biomass into predator biomass because under low densities the predator may never encounter the prey.

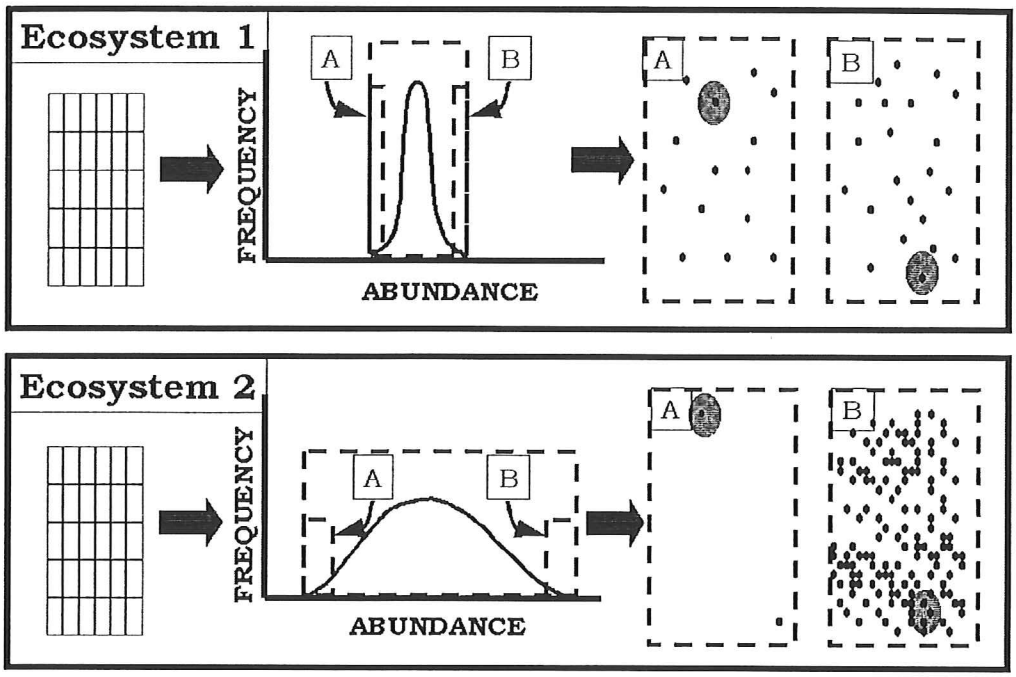

Figure 1.7 The impact of individual interactions on the ecosystem may be significant. In Ecosystem 1, interaction between neighboring cells may be treated as a constant whereas in Ecosystem 2, the interaction between individuals of neighboring cells must be taken into account since it is possible individuals may not meet in order to take part in selected population dynamics.

1.4.2 **Ecosystem-Level Risk Assessment**

Population models are used as the basis of risk assessment for issues commonly involving individual species and the effects of contaminants and toxic materials (or other stressors) on population numbers. Population models vary in complexity, but typically a modeler must estimate fecundity, density dependence, and survival, either for ages or stages of the population. Population dynamics are

simulated by randomly selecting the necessary coefficients from a distribution of coefficients. Typically, a baseline condition is simulated multiple times to obtain a distribution of results that will serve as the basis of comparison (Figure 1.8). The model runs are summarized as the probability, or risk, that at a reference time the population abundance will decrease below a certain threshold value.

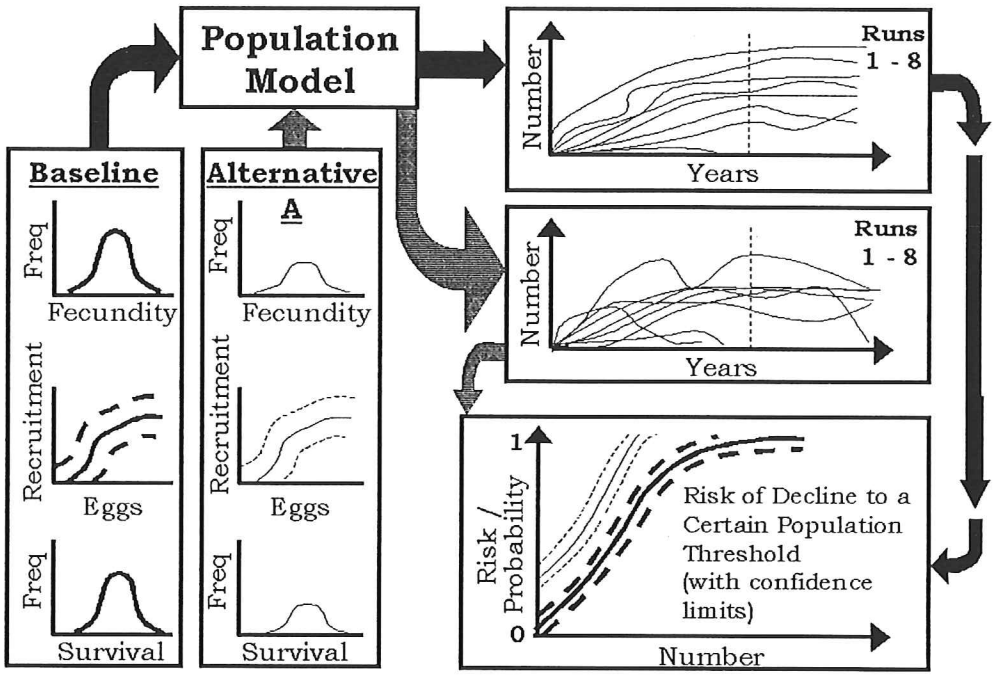

Figure 1.8 Schematic of the population risk assessment process.

The effects of a stressor are predicted using the same steps except that the coefficients used to estimate population dynamics are adjusted to represent the effects of the stressor. For example, fecundity or survival may be reduced in the presence of the stressor (Figure 1.8). Multiple model runs with coefficients selected from the

revised distributions are then used to develop a family of model runs that includes the effects of the stressor. The model runs that include the effects of the stressor can then be summarized and compared to the baseline runs in terms of the changes in risk associated with the stressor compared to the baseline.

CEL Hybrid Ecological Models allow for a more detailed analysis of the cause and effect relationships behind population estimates. For example, a lake may contain a site in which sediments are contaminated with mercury. This same lake may contain a population of striped bass, a fish whose distribution within a lake is determined by water temperature and dissolved oxygen stratification. In a standard population model based risk assessment, a general comparison between the baseline (no contaminated sediments) and contaminated sediments scenario results would be used to evaluate the effects of the stressor. However, a CEL Hybrid Ecological Model would allow other aspects, such as reservoir operations, to be included in the risk assessment by linking the movement of striped bass to stratification patterns within the reservoir. The CEL Hybrid Ecological Model can then be used to estimate dose-exposure for the fish (how much time each fish spends in areas of different stressor concentrations) and, thereby, refine the effects of the stressor. Alternatively, the CEL Hybrid Ecological Model can be used to evaluate the impact of various management scenarios (e.g., reservoir operations) on patterns in the physicochemical environment (e.g., stratification

patterns), which, in turn, may affect the dose-exposure histories of the organisms. For instance, in aquatic systems a CEL Hybrid Ecological Model could be used to determine if raising the pool elevation by two feet minimizes the dose-exposure of striped bass in the reservoir. CEL Hybrid Ecological Models can be used to consider and manage stressors in an ecosystem context and tradeoff the effects of natural stressors, such as naturally occurring elevated temperatures or low dissolved oxygen levels, against the effects of contaminants or toxic materials.

1.4.3 **Virtual Sampling**

CEL Hybrid Ecological Models create a virtual ecosystem that can be sampled using virtual sampling gear. Unlike Eulerian-based models in which individual organisms have to be converted into biomass, CEL Hybrid Ecological Models can simulate organisms directly and individually, and the virtual reality of the model can be sampled with virtual sampling gear to allow direct comparison with real-world sampling gears, without transformations or conversions. Virtual sampling gears can be burdened with all of the assumptions and inadequacies of real-world sampling gears to generate samples that have similar statistical characteristics (mean and variance) as real-world samples. Therefore, the step of transforming the abundance of a target species population from numbers per life-stage per meter to a variable such as kg/m^3 is avoided along with the associated loss of information. Furthermore, tradeoffs in

sampling efficiency between different sampling gear types can be evaluated using CEL Hybrid Ecological Models.

1.5 **Summary and Conclusions**

1.5.1 **Theoretical Considerations**

The best model for capturing the full suite of ecosystem processes is the ecosystem itself. Unfortunately, such detailed replication of natural ecosystems is not possible. In lieu of complete duplication, ecosystem modelers attempt to capture the most important aspects of ecosystem structure and processes in numerical models, fully realizing that the model is nothing more than a highly simplified version of reality.

In the existing state-of-the-art, modelers have one of two major conceptual pathways that they follow in an attempt to mathematically recreate natural spatiotemporal ecological mechanisms. A modeler may take the Eulerian approach or the Lagrangian approach. However, either approach, by itself, is an incomplete representation of reality since the strengths of the other perspective are unavailable. Therefore, neither approach by itself can serve as a guide to achieving a more complete understanding of ecosystem structure and function.

ELMs and, in particular, CEL Hybrid Ecological Models, provide a more complete perspective for understanding ecosystems than either Eulerian or Lagrangian approaches by themselves. The coupled approach has the potential for a total description of

complicated processes that neither approach can achieve by itself (Tran-Son-Tay *et al.*, 1998). Particle-tracking logic can be used as a gateway to move back and forth between the two modeling frameworks as needed. By coupling Eulerian and Lagrangian frameworks into a single modeling framework, ecosystem scientists have the potential for getting closer to a first principles understanding of natural systems since the coupled framework can build on the unique strengths of each perspective.

1.5.2 **Representing Different Temporal and Spatial Scales**

Levin (1992) identifies determination of scale and pattern as the central problem facing ecologists in their studies of ecosystems. Presently, CEL Hybrid Ecological Models offer some advantages over either mass-balance or population models separately because CEL Hybrid Ecological Models perform simulations at the scale of the Eulerian-based model and at the scale of the Lagrangian-based model. The scales at which each of the two submodels in a CEL Hybrid Ecological Model run do not have to be the same. Therefore, CEL Hybrid Ecological Models tend to be bi-scale with the Eulerian-based model running at a relatively fine temporal and spatial scale and the Lagrangian-based model (or, at least, parts of it) running at larger temporal and spatial scales.

CEL Hybrid Ecological Models, even though they may have more complete scale representation than their component submodels, still must generally operate over a limited range of

scales because of limitations in computational resources. Therefore, application of CEL Hybrid Ecological Models will require some judgment on the part of the modeler to optimally scale a simulation to address a particular issue. Presently, it is not possible to include more than a limited number of species populations in a CEL Hybrid Ecological Model because description of movement in the model is computationally demanding.

1.5.3 **Conclusions**

CEL Hybrid Ecological Modeling is a new method for coupling the Eulerian and Lagrangian modeling frameworks so the higher trophic levels of an ecosystem can be systematically and realistically simulated. CEL Hybrid Ecological Models have the potential to partially address the problems identified by Alewell and Manderscheid (1998), that some biological processes are inherently too difficult to simulate, and by Turchin (1997), that full spatiotemporal analysis is conceptually difficult. The study of animal behavior is challenging because behavior is often an integrated response to a complex situation (Schilt and Norris, 1997). CEL Hybrid Ecological Models provide a systematic means for segregating these integrated responses into their component parts so that animal behavior can be better understood for development of improved natural resources management.

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Simulating Mobile Populations in Aquatic Ecosystems Using a CEL Hybrid Ecological Model: Algorithm Development

2.1 Abstract

Eulerian-Lagrangian methods (ELMs) provide a means to achieve a more realistic simulation of higher trophic level aquatic species movement behavior in dynamic systems. Although the Lagrangian framework is preferred, for several reasons, for simulating the movement of individuals in a biological population, movement behavior dynamics are often forced into the Eulerian framework used in simulating physicochemical regimes, e.g., flow and water quality fields. I develop a couple, the Numerical Fish Surrogate, that allows movement behavior and other biological dynamics best simulated with a Lagrangian framework to be incorporated into Eulerian-based physicochemical simulation models.

The Numerical Fish Surrogate (NFS) is, at its core, a particle-tracking algorithm enhanced with behavioral, or stimuli-response, rules. The NFS is the translation mechanism that mediates between sensory inputs from the physicochemical environment and emergent behavior. The resulting modeling framework, the Coupled Eulerian-Lagrangian Hybrid (CEL Hybrid) Ecological Modeling System, has improved capabilities for handling the movement behavior, and other dynamics, of higher trophic level species in a realistic and systematic manner.

2.2 **Introduction**

Aquatic ecosystems have emergent properties that can only be assessed when the system is considered in its entirety. Decision-support tools, therefore, must be capable of capturing, at the very least, a select number of critical ecological processes in order to realistically capture the impact landscape and waterscape modifications may have on aquatic ecosystems. Presently, a number of tools exist for simulating the impact various activities (e.g., dam and reservoir operation, construction, dredging) have on a number of these critical ecosystem processes (e.g., hydraulics, water quality, lower trophic levels). However, few tools exist that capture the impact of such activities on higher trophic level aquatic species, due to changes in the physicochemical regimes (i.e., hydraulic and water quality fields), much less the full suite of integrated and synergistic relationships that exist between physicochemical regimes, lower trophic levels, and higher trophic levels (Tischendorf, 1997).

The obstacle to achieving such simulation capacity is two-fold: the lack of a robust translation mechanism and the absence of an appropriate modeling framework. First, few algorithms exist that have the capacity to realistically and systematically translate the mechanisms that mediate between the sensory input of higher trophic levels, e.g., from flow and water quality fields, and emergent behavior. Second, no systematic modeling framework has been

employed that allows for routine, systematic, and realistic handling of such higher trophic level simulations as well as the various feedback processes. Ideally, the modeling framework would also be conducive to investigative processes (e.g., data mining) so, among other things, the quantitative and qualitative information acquired from field research would be directly and immediately compatible with the method used to replicate, or simulate, the ecological process studied.

In this chapter, I describe an algorithm, the Numerical Fish Surrogate, and how it is used to simulate/translate mechanisms that mediate between sensory inputs and emergent behavior (Warburton, 1997) of a higher trophic level cool water fish species. This description is critical because the Numerical Fish Surrogate (NFS) is also the computational doorway allowing modelers to move freely between the Eulerian modeling framework, typical of most hydraulic and water quality models, and the Lagrangian modeling framework, preferred for simulating the movement of animals (Turchin, 1997). The NFS is the centerpiece of the CEL Hybrid Ecological Modeling System (Chapter 1) because it allows the modeler to exploit the strengths of each modeling framework. Application and evaluation of the NFS in simulating the movement behavior of a cool water fish species is detailed in Chapter 3.

2.2.1 **CEL Hybrid Ecological Modeling**

The computer models used by engineers, to simulate physicochemical regimes, and by biologists, to simulate animal movement, often differ in the modeling framework employed. Physicochemical models used to simulate hydraulic and water quality processes employ the Eulerian framework (i.e., a framework centered on a point fixed in space) so that fluxes of mass and energy may be balanced in both time and space, to ensure conservation of mass, energy, and momentum. In contrast, many biological population models used to simulate animal movement employ the Lagrangian framework (i.e., a framework centered on the individual object) and are vector-based to enhance compatibility with tracking data and analytical treatments of movement processes (Tischendorf, 1997).

The use of different modeling frameworks creates a disconnect between the existing engineering and biological modeling abilities. For instance, population models must often ignore spatial heterogeneity because it is difficult to incorporate into the Lagrangian framework. At the same time, engineers often incorporate population characteristics, such as the number and sizes of individuals in a population, by converting them into spatially-integrated surrogate variables (e.g., cell biomass) so they can be incorporated into the Eulerian, or compartment-based, models. However, the use of surrogate variables constrains an ecosystem-level assessment because most surrogate variables (e.g.,

biomass) cannot capture information needed to realistically simulate other important population attributes (e.g., size-specific egg production).

The Coupled Eulerian-Lagrangian Hybrid (CEL Hybrid) Ecological Modeling System (Chapter 1) circumvents this problem by separating those processes best simulated using a Eulerian framework from those best simulated using a Lagrangian framework. CEL Hybrid Ecological Models use a Lagrangian framework to maintain the integrity of individuals as they move through simulated space while concurrently using the Eulerian framework to simulate the physicochemical and other characteristics of the system over time and space. The NFS, a particle-tracking algorithm enhanced with behavioral rules, translates the sensory inputs to biological individuals, either Eulerian-based quantities (e.g., temperature) or Lagrangian-based quantities (e.g., nearest-neighbor), into emergent Lagrangian-based movement behavior. The framework also allows for the translation of Lagrangian-based quantities (e.g., number and size of individuals) into Eulerian-based quantities (e.g., mass of nutrient generation or depletion due to uptake, excretion, etc.) so that biological processes may be feed back into the physicochemical simulation. The addition of existing models/algorithms that capture aspects of behavioral ecology (e.g., Nonacs *et al.*, 1994) and bioenergetics (e.g., Schindler and Eby, 1997) would complete the CEL Hybrid Ecological Modeling System.

2.3 **Development of the Numerical Fish Surrogate**

Development of the NFS was based on position data sets available for blueback herring (*Alosa aestivalis*) in the dynamic, heterogeneous environment of J. Strom Thurmond (JST) Lake, a reservoir on the Savannah River between Georgia and South Carolina. This cool water fish species was selected because its response to temperature and dissolved oxygen stratification and hydraulic patterns is representative of the response of many cool and cold water fish species found in lakes, streams, and estuaries. Realistic simulation of the movement dynamics of this species will serve as a model for similar species whose distribution may be impacted by environmental changes associated with water resources development, particularly in settings where the changes in the hydrodynamic and water quality regimes can be accurately simulated.

2.3.1 **Procedure**

Development of the NFS consisted of a series of integrated steps, including: 1) obtaining suitable field data for quantitatively describing the movement of the target fish species, 2) obtaining a calibrated and verified hydrodynamic and water quality model, 3) integrating a particle-tracking algorithm into the hydrodynamic and water quality model, 4) developing stimuli-response rules for the target fish species to variables simulated in the model, 5) simulating

the hydrodynamic and water quality regimes along with the movement of virtual fish, and 6) presenting model results in a format consistent in scale and resolution to the field data obtained in step 1.

2.3.1.1 *Step 1 – Fish Position Field Data.*

Fish positional data used for the NFS calibration were obtained from gillnet and dual-beam hydroacoustic surveys (Dennerline and Degan, in prep) conducted during August 1996. More specifically, the positional data used in this study included:

1. Mobile fisheries hydroacoustic surveys - a sampling method in which a specialized SONAR system is deployed from a boat, which runs transects back and forth across a water body. The results of mobile surveys can be used to locate fish in three-dimensions within a lake.
2. Gillnet surveys - a sampling method in which a series of nets are used to capture fish. Each net is made up of several separate panels, with each panel having a different mesh size. The result is a series of nets having a graded series of different mesh sizes, which increases the probability of catching fish of various sizes. Gillnets are typically used to indicate the presence or absence of fish species susceptible to gillnetting.

2.3.1.2 *Step 2 – Hydrodynamic and Water Quality Model.*

The hydrodynamic and water quality component of the CEL Hybrid Ecological Model was CE-QUAL-W2 Version 3.0 (Cole and Tillman, in prep). CE-QUAL-W2 is a two-dimensional, laterally averaged, dynamically-linked hydrodynamic and water quality model. It has been under continuous development since the mid-1970s. CE-QUAL-W2 has been applied to numerous lakes, estuaries, rivers, pit lakes, and reservoirs (e.g., Cole and Tillman, 1996).

The FORTRAN structure of CE-QUAL-W2 was used as the basis for the NFS. The NFS was coded into CE-QUAL-W2 as a series of 14 FORTRAN subroutines dynamically linked to the main CE-QUAL-W2 program. This link allowed the NFS to run in step with the hydrodynamic and water quality algorithms, thus avoiding the need for computer disk space to store flow and water quality output.

CE-QUAL-W2 defines horizontal velocity ($U_{k,i}$) at the right vertical face, vertical velocity ($W_{k,i}$) at the lower horizontal face, and water quality constituents ($WQ_{k,i}$) at the center of each respective laterally-collapsed grid cell located at the intersection of vertical layer k and longitudinal segment i (Figure 2.1). For computational convenience, and to facilitate graphics post processing, all flow and water quality information was moved (i.e., interpolated) and redefined at the upper-left node for each respective grid cell. 3rd Order Newton interpolation polynomials (Chapra and Canale, 1998)

were used to "move" velocity information from cell faces to the node, and bilinear splines (Spath, 1995) were used to "move" water quality information from the cell center to the node (Figure 2.1).

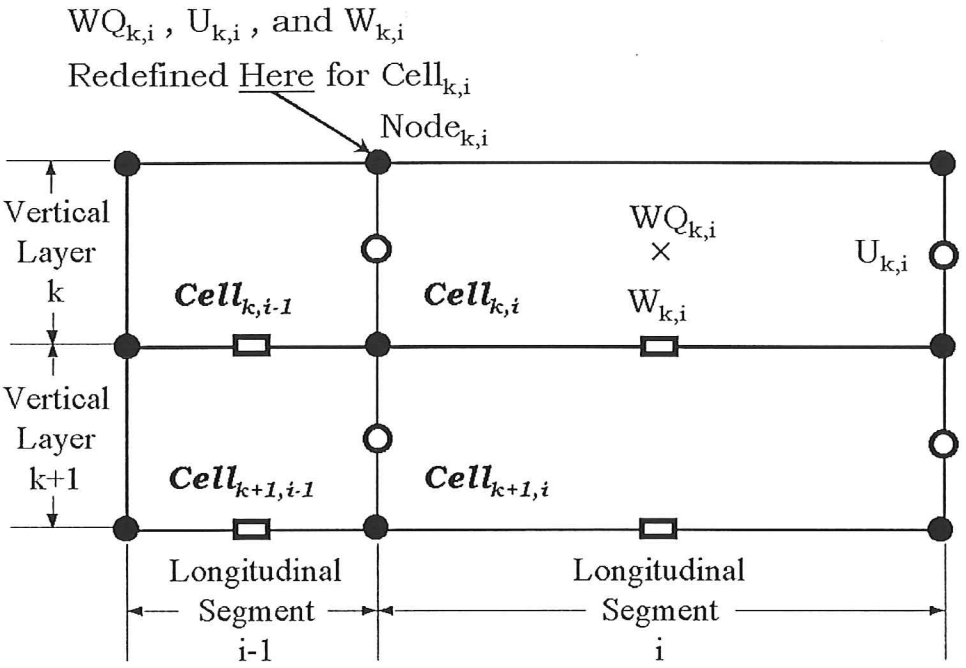


Figure 2.1 Horizontal velocity ($U_{k,i}$), vertical velocity ($W_{k,i}$), and water quality constituent values ($WQ_{k,i}$) in CE-QUAL-W2 were defined at the center of the right vertical face (O), at the center of the lower horizontal face (□), and at the cell center (X), respectively, for each grid $Cell_{k,i}$. For computational convenience, these values were moved (i.e., interpolated) and redefined at the upper-left node (•) of the corresponding $Cell_{k,i}$.

2.3.1.3 *Step 3 - Particle-Tracking Algorithm.*

The particle-tracking algorithm used as the foundation for the NFS was developed by the U.S. Army Engineer Waterways Experiment Station (Chapman *et al.*, 1994) to predict the transport and fate of floatables and suspended and dissolved materials in three dimensions. The algorithm was simplified for use in CE-QUAL-W2 by deleting portions of the model relating to surface transport of floatables and suspended and dissolved materials. In addition, transport equations for lateral movement were deleted because CE-QUAL-W2 only computes forcing functions in the longitudinal and vertical directions. Figure 2.2 describes how the particle-tracking algorithm defines the exact location of each particle in CE-QUAL-W2.

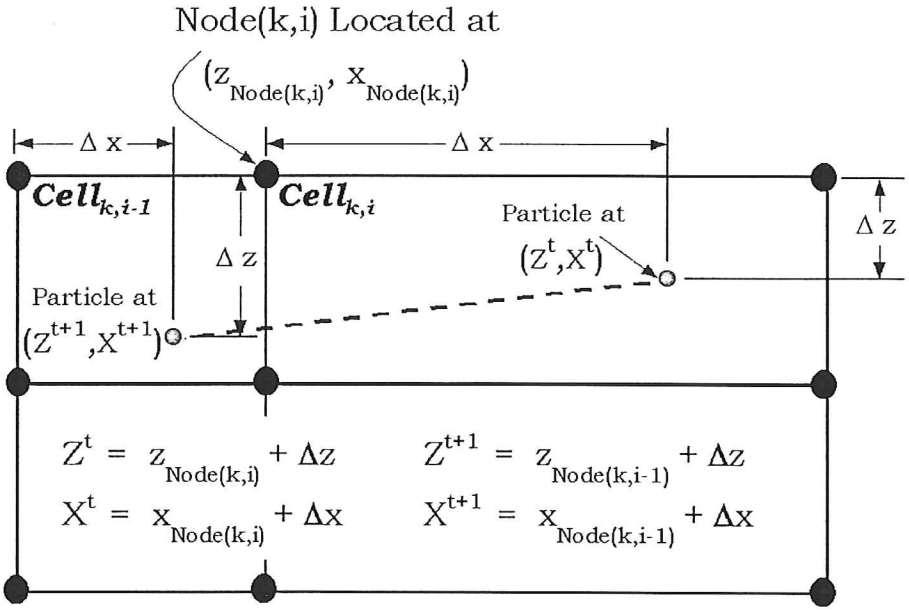


Figure 2.2 Scheme for describing the exact positions of a hypothetical particle at times t and t+1 in CE-QUAL-W2.

Equations in Chapman *et al.* (1994) were simplified for use in CE-QUAL-W2 as follows:

$$X^{t+1} = X^t + U^t(Z^t,X^t) * \Delta t \quad (2.1)$$

$$Z^{t+1} = Z^t + W^t(Z^t,X^t) * \Delta t \quad (2.2)$$

where: X^{t+1} = Longitudinal position, $x_{Node(k,i)} + \Delta x$, of particle at time t+1, in meters

Z^{t+1} = Vertical position, $z_{Node(k,i)} + \Delta z$, of particle at time t+1, in meters

X^t = Longitudinal position, $x_{Node(k,i)} + \Delta x$, of particle at time t, in meters

Z^t = Vertical position, $z_{Node(k,i)} + \Delta z$, of particle at time t, in meters

$U^t(Z^t,X^t)$ = Interpolated horizontal flow velocity (m/s) at location (Z^t,X^t)

$W^t(Z^t,X^t)$ = Interpolated vertical flow velocity (m/s) at location (Z^t,X^t)

Δt = Time interval between time t and time t+1, in seconds.

After X^{t+1} and Z^{t+1} were calculated, boundary checks were performed to determine if the particle's new position exceeded either the longitudinal or vertical dimensions of its current cell or any

system boundary. If the particle's new position exceeded the longitudinal or vertical dimensions of the current cell, an algorithm was activated to determine the appropriate cell in which to place the particle. Once the appropriate cell was found, k, i, $Node_{k,i}$, $x_{Node(k,i)}$, $z_{Node(k,i)}$, Δx, and Δz were updated for the particle and stored. If the particle exceeded a system boundary (e.g., a water surface, upstream, downstream, or lake bottom boundary), special rules were triggered to reflect the particle.

2.3.1.4 *Step 4 – Developing stimuli-response rules.*

Particle-tracking algorithms only simulate the passive movement of objects in a flow field. However, recognizing that movement decisions of an individual fish can be viewed as a balance of forces (Okubo, 1980), in particular a set of attractions to and repulsions from various sources or foci (Parrish and Turchin, 1997), behavioral cues, or stimuli-response rules, can then be added to the particle-tracking algorithm to emulate the fish's movement behavior. Enhancement of the particle-tracking algorithm through the addition of stimuli-response rules, which when taken as a whole dictate the pattern of movement (Schilt and Norris, 1997), creates a virtual organism capable of making individual movement decisions related to the spatial information as provided by the Eulerian-based model (Tischendorf, 1997) in a way that emulates the behavior of real fish.

Specifically, an additional term was added to each passive transport equation to account for the speed of volitional swimming in the X- and Z- directions (U_{fish}, W_{fish}) in response to environmental gradients. The movement of fish could then be described as the resultant of passive and volitional movement (Figure 2.3). The passive transport equations (i.e., equations 2.1 and 2.2) were expanded as follows:

$$X^{t+1} = X^t + (U^t(Z^t,X^t) + U^t_{fish}) * \Delta t \quad (2.3)$$

$$Z^{t+1} = Z^t + (W^t(Z^t,X^t) + W^t_{fish}) * \Delta t \quad (2.4)$$

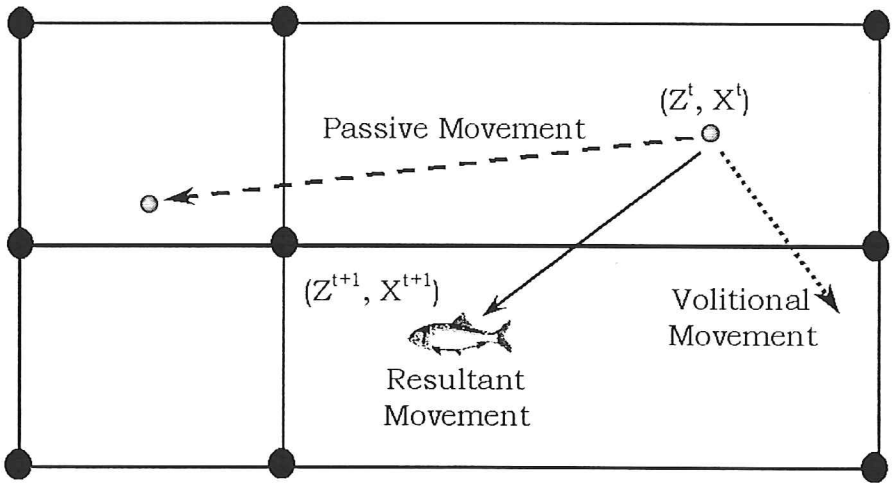


Figure 2.3 The movement of fish is described as the resultant of passive and volitional movement.

The speed and direction of volitional swimming was determined using stimuli-response rules related to the spatial context of the individual's position (Tischendorf, 1997). These

stimuli-response rules were developed based on Niche theory and couched as a simplified version of a Markov Chain behavioral model (Haccou and Meelis, 1992). Rules translated the presence of environmental gradients into emergent behavior by: a) developing a sensory ovoid representative of the area blueback herring would search, during each time step, to determine various environmental gradients, b) calculating gradients of velocity, temperature, and dissolved oxygen, c) determining the movement response to each environmental gradient independently, d) normalizing and weighting each environmental gradient and having the virtual fish select a variable (i.e., a gradient or a random number) to respond to, and e) eliciting volitional movement by combining the virtual fish's "motivation to move" with its maximum swim speed decremented for non-optimal water quality conditions.

2.3.1.4.1 *Development of a Sensory Ovoid.*

Niche theory states that biological species have ecological "preferences," meaning that they are found in areas where environmental variables have some "optimal" value (Legendre *et al.*, 1997). Literature on blueback herring (e.g., Isely, 1996; Thomas *et al.*, 1992; Osteen *et al.*, 1989; West *et al.*, 1988; Dadswell, 1985; Meador *et al.*, 1984; Fay *et al.*, 1983; Pardue, 1983; Skjeveland, 1982; Loesch and Lund, 1977) suggests that moderate water temperatures (e.g., 14°C-27°C), dissolved oxygen, and fast-flowing water are important factors that attract blueback herring,

particularly for spawning. Gradients of these environmental variables were used together with a random term, used to generate dispersion in the virtual fish population, to elicit volitional movement.

To determine appropriate gradients, a sensory ovoid is constructed around each 'particle' as an estimate of how much area (two-dimensional laterally-collapsed volume) an adult blueback herring would search in order to select its direction of movement, within a single time step of the model. The limit of the sensory ovoid represents the maximum distance that a blueback herring could be expected to search in the X- or Z-direction in one time step. The aspect ratio of the sensory ovoid was distorted so that the horizontal axes (Δx_1, Δx_2) were substantially larger than the vertical axes (Δz_1, Δz_2) (Figure 2.4) since field observation indicates that blueback herring swim primarily in the longitudinal direction. Among other things, the limit of the sensory ovoid is dependent on the time step used. Size of the sensory ovoid will increase with an increasing time step so that time step intervals of minutes will be associated with larger sensory ovoids than time step intervals of seconds.

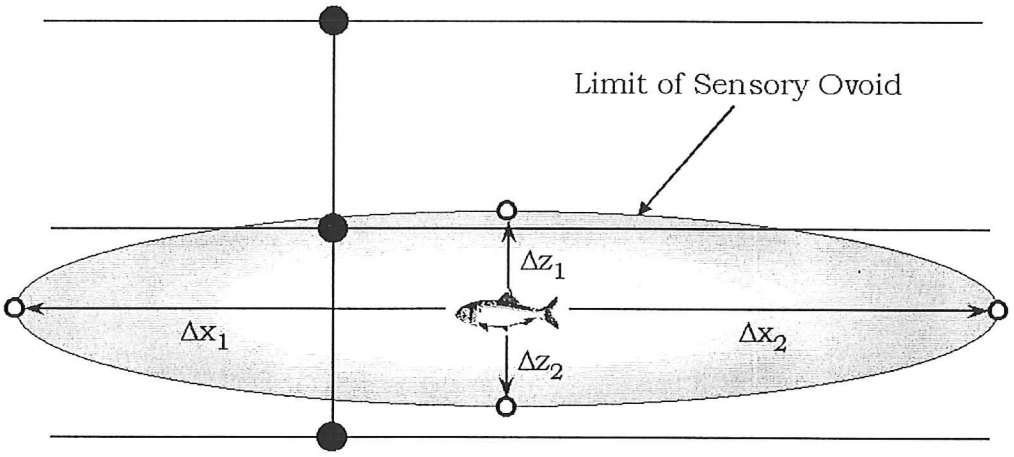


Figure 2.4 Diagram of a virtual blueback herring sensory ovoid. The sensory ovoid can extend into other cells.

A scaled sensory ovoid is calculated using the following equations:

$$\Delta x_1^t = \text{FBDYSEARCH} * \text{FSIZE} * \text{RRR}^t \quad (2.5)$$

$$\Delta x_2^t = \text{BBDYSEARCH} * \text{FSIZE} * \text{RRR}^t \quad (2.6)$$

$$\Delta z_1^t = \text{UBDYSEARCH} * \text{FSIZE} * \text{RRR}^t \quad (2.7)$$

$$\Delta z_2^t = \text{DBDYSEARCH} * \text{FSIZE} * \text{RRR}^t \quad (2.8)$$

where: FSIZE = Size (i.e., length) of the fish (m)

FBDYSEARCH = The number of body lengths (FSIZE) in front of the fish that it can search during a time interval

BBDYSEARCH = The number of body lengths (FSIZE) behind the fish that it can search during a time interval

UBDYSEARCH = The number of body lengths (FSIZE) above the fish that it can search during a time interval

DBDYSEARCH = The number of body lengths (FSIZE) below the fish that it can search during a time interval

RRR^t = Random number between 0.0 and 1.0

I assume that blueback herring determine flow and water quality gradients from their current location to a range equal to or less than the limit of the sensory ovoid. The distances in X and Z along which gradients are calculated are obtained from a random uniform distribution scaled so that the minimum distance is 0.0 and the maximum distance over which gradients can be determined is defined by the limit of the sensory ovoid.

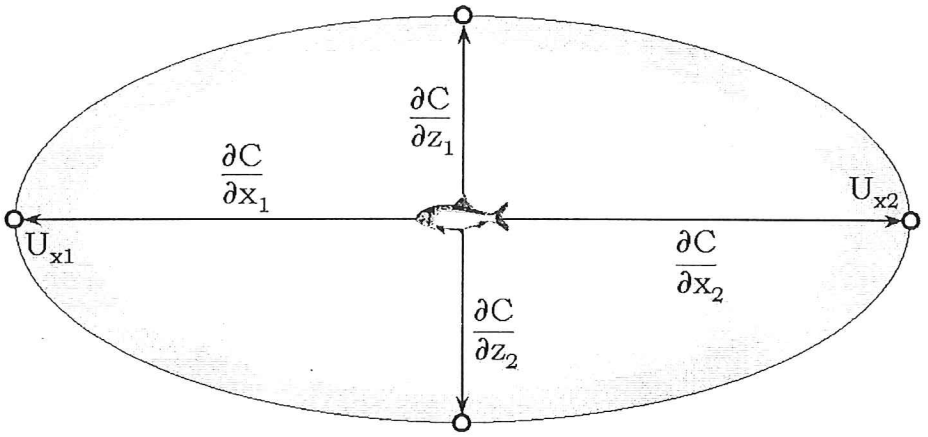
The notion of a sensory ovoid also allows the NFS to adjust to different models that may vary in their scales of discretization, time steps, and degrees of distortion between axes. The CE-QUAL-W2 representation of JST Lake uses a scale of discretization of 0.5 or 1.0 m in the Z-direction and 1000 m to 9000 m in the X-direction and a time step ranging between one and three minutes. The aspect ratio of the grid cells is such that they are about 10,000 times longer than thick.

The time step of the NFS can vary independently of the time step of CE-QUAL-W2. The time step of CE-QUAL-W2 is selected to

keep the solutions to hydrodynamic and water quality equations as stable and accurate as possible. The time step used by the NFS, however, can be set to any time interval greater than or equal to that used by CE-QUAL-W2.

2.3.1.4.2 *Calculation of Environmental Gradients.*

A bilinear spline interpolation function (Spath, 1995) was used to determine the horizontal and vertical gradients of the two velocity components, temperature, and dissolved oxygen between the initial fish position and the four cardinal points of the scaled sensory ovoid boundary. The interpolation scheme can operate across cell boundaries so gradients can be determined even if the boundary of the sensory ovoid exceeds the edges of the Eulerian cell in which the fish is located. Since bilinear splines were used, gradients in the same plane will only be different if opposing edges of the sensory ovoid lie in different Eulerian cells. The direction the fish is facing (i.e., upstream or downstream) is recorded so that the user can specify a sensory ovoid with different distances to the forward and backward boundary. The following gradients are determined (Figure 2.5):



C = { Horizontal Velocity (U), Vertical Velocity (W),

Temperature (T), Dissolved Oxygen (DO) }

Figure 2.5 Separate linear gradients are calculated between the edge of the scaled sensory ovoid and the fish location for horizontal velocity, vertical velocity, temperature, and dissolved oxygen.

2.3.1.4.3 *Prioritizing Among Variables.*

To begin translating the presence of environmental gradients into emergent behavior, each environmental gradient was analyzed in each plane (i.e., horizontal and vertical) to determine what the preferred movement direction would be if the fish were responding only to that environmental variable. Of the environmental gradients, temperature gradients and the horizontal gradient of horizontal velocity ($\partial U/\partial x_1$ and $\partial U/\partial x_2$) required special attention.

The diel vertical migration of blueback herring (Loesch *et al.*, 1982) has been attributed to, among other things, water temperature, light intensity (Jessop, 1990; Loesch, 1987), and the diel movement of zooplankton (Pardue, 1983; Neves, 1981).

Blueback herring density is greater at the surface at night than at midday (Meador *et al.*, 1984; Bulak, 1979; Wang and Kernehan, 1979). To best capture this movement behavior, temperature was used as a surrogate variable to account for not only the influence of temperature on the diel movement of blueback herring, but also the influences of light intensity and zooplankton. Diel movement could then be simulated by programming the NFS so that virtual blueback herring seek out different optimum 'temperatures' during the day than at night. The main reason for treating the diel movement behavior as a response to temperature was that only temperature was available from the water quality model (CE-QUAL-W2), although it is possible, if not likely, that light intensity and zooplankton densities are correlated with water temperature and would, if proven, further justify the use of a surrogate variable.

Unlike other variables whose gradients could be proportioned to obtain a surrogate value for the motivational state of an individual to move, the horizontal gradients of horizontal velocity (both forward, $\partial U/\partial x_1$, and behind, $\partial U/\partial x_2$, the fish) did not provide the spatial and temporal attributes necessary to produce "motivational" values leading to realistic fish movement behavior. On the other hand, actual velocity values did provide the necessary spatial and temporal attributes. For this reason, the horizontal gradients of horizontal velocity were replaced with actual velocity values. In place of $\partial U/\partial x_1$ and $\partial U/\partial x_2$ were substituted the values of horizontal velocity at the forward edge (U_{x1}) and the backward

edge (U_{x2}) of the scaled sensory ovoid, respectively. Preliminary assessment of the benefit in making additional substitutions for the remaining components of velocity showed only marginal improvement in model performance, mainly because other factors were dominant in eliciting modeled fish movement.

A 'gradient selection logic' is employed once gradients for each variable are determined in the four principle directions. That is, a suite of tests is performed on the gradients to select the horizontal and vertical directions leading to improved habitat conditions for the target species life stage. No gradient is chosen if conditions around the fish provide habitat of less quality than the fish's present location. The selection logic is summarized as follows, with an illustration of possible results following in Table 2.1:

$(\partial U/\partial x)_p^t$ = Of the velocities $\{|U_{x1}|, |U_{x2}|\}$, whichever is greater

$(\partial U/\partial z)_p^t$ = Of the gradients $\{\partial U/\partial z_1, \partial U/\partial z_2\}$, the one leading to more desirable conditions

$(\partial W/\partial x)_p^t$ = Of the gradients $\{\partial W/\partial x_1, \partial W/\partial x_2\}$, the one leading to more desirable conditions

$(\partial W/\partial z)_p^t$ = Of the gradients $\{\partial W/\partial z_1, \partial W/\partial z_2\}$, the one leading to more desirable conditions

$(\partial T/\partial x)_p^t$ = Of the gradients $\{\partial T/\partial x_1, \partial T/\partial x_2\}$, the one leading to more desirable conditions

$(\partial T/\partial z)_p^t$ = Of the gradients $\{\partial T/\partial z_1, \partial T/\partial z_2\}$, the one leading to more desirable conditions

$(\partial DO/\partial x)_p{}^t$ = Of the gradients $\{\partial DO/\partial x_1, \partial DO/\partial x_2\}$, the one leading to more desirable conditions

$(\partial DO/\partial z)_p{}^t$ = Of the gradients $\{\partial DO/\partial z_1, \partial DO/\partial z_2\}$, the one leading to more desirable conditions.

Table 2.1 An Illustration of Results from Prioritizing Among Variables.

Variable	Preferred Movement in Horizontal Plane	Preferred Movement in Vertical Plane
Horizontal Velocity (U)	Forward	Upward
Vertical Velocity (W)	Forward	Downward
Temperature (T)	Neither[1]	Downward
Dissolved Oxygen (DO)	Backward	Upward

[1]'Neither' will result if the current condition is more desirable than neighboring conditions.

2.3.1.4.4 *Prioritizing Between Variables.*

At each time step, only one of the environmental variables may influence fish movement. We assume that the speed and direction of movement for each virtual fish is determined by the variable exhibiting the largest gradient. To determine this gradient, the NFS inspects the output of the Eulerian component of the CEL Hybrid Ecological Model to determine the largest gradient for each

environmental variable. The NFS then uses a "maximum response gradient" (defined for each environmental variable in the input) to normalize the gradients to the range [-1,1]. Occasional normalized gradients exceeding |1.0| are truncated. The following formulation was used to normalize variable gradients:

$$(\partial C/\partial d)^t_n = (\partial C/\partial d)_p{}^t \; / \; |\partial C/\partial d|_{max} \qquad (2.9)$$

where: C = {Horizontal velocity (U), vertical velocity (W), temperature (T), dissolved oxygen (DO)}

d = {Horizontal plane (x), vertical plane (z)}

$(\partial C/\partial d)^t_n$ = Normalized gradient of variable "C" in the "d" plane

$(\partial C/\partial d)_p{}^t$ = Preferred gradient of variable "C" in the "d" plane, as calculated in 2.3.1.4.3

$|\partial C/\partial d|_{max}$ = Gradient of variable "C" in the "d" plane likely to induce the maximum movement response in a blueback herring.

The "maximum response gradient" values inputted for each variable remain constant throughout the entire simulation. Once the variable gradients are normalized, they can then be compared against one another, on equal footing, as well as compared to a random number that ranges from -1 to 1. The normalized gradients and the random number are then weighted. The environmental

variable weights below permit unequal attention/response to different variables:

$$(\partial C_w/\partial d)^t = (\partial C/\partial d)^t{}_n * C_w \qquad (2.10)$$

where: $(\partial C_w/\partial d)^t$ = Weighted normalized gradient of variable "C" in the "d" plane, or weighted random number

$(\partial C/\partial d)^t{}_n$ = Normalized gradient of variable "C" in the "d" plane, or unweighted random number with range [-1,1]

C_w = Weight of variable "C" or random number representing influence on fish movement behavior; range [0,1].

I assume that biota are more likely to respond to environmental gradients when subjected to unsuitable habitat conditions than when located in optimum habitat. To account for this behavior, variable gradient values for temperature and dissolved oxygen are decremented if habitat conditions at the fish location are near optimum. Also, blueback herring are a pelagic species (i.e., they swim continuously), so to accommodate this behavior the random term is adjusted so fish moving randomly (i.e., not responding to any environmental stimulus) continue to move at some constant swimming speed.

The absolute value of each gradient value is taken after variable gradient values have been normalized, weighted, and decremented by the NFS. Virtual fish are programmed to then select one of the absolute values or the random number, whichever is greater, for each plane of movement. Once a gradient value or random number is chosen, the value's sign is restored with positive values resulting in movement forward and negative values resulting in movement backwards. An illustration of results that could be obtained from an analysis is shown in Table 2.2.

Table 2.2 An Illustration of Results from Prioritizing Between Variables.

Variable	Preferred Movement in Horizontal Plane	Preferred Movement in Vertical Plane
Horizontal Velocity (U)	-	-
Vertical Velocity (W)	-	-
Temperature (T)	-	Downward
Dissolved Oxygen (DO)	-	-
Random Number	Forward	-

2.3.1.4.5 *Summarizing Fish Movement Simulation.*

At this point, all elements exist to simulate movement behavior of blueback herring. The movement methodology is based

on using the values calculated in cross-variable analysis (2.3.1.4.4) as a surrogate for "urgency", or the motivational state of an individual (Warburton, 1997) to move from its current position. These urgency values ($X_{URGENCY}$, $Z_{URGENCY}$) range from –1 to 1, with higher absolute values (0 to 1) eliciting greater movement responses from virtual fish. All movement in the lateral dimension is random because no flow or water quality variation is computed. Lateral movement must be computed to take advantage of a bookkeeping scheme developed specifically for the NFS that allows virtual fish to move into tributaries (i.e., branches). In short, the following equivalencies are made:

$$X^t_{URGENCY} \equiv (\partial C_w/\partial x)^t \quad (2.11)$$

$$Z^t_{URGENCY} \equiv (\partial C_w/\partial z)^t \quad (2.12)$$

Once urgency is determined, the speed at which the virtual fish 'swims' must be determined. I assume the speed at which fish swim is related to both the fish's urgency to move and its maximum swimming speed. In order to proceed with this assumption, maximum swimming speed must be determined. First, the physiological maximum swimming speed (i.e., the fastest a fish can swim under optimum conditions; $U_{fish,MAX}$, $W_{fish,MAX}$) is calculated from inputted values as:

$$U_{fish,MAX} = FSIZE * MXXSPDL \quad (2.13)$$

$$W_{fish,MAX} = FSIZE * MXZSPDL \quad (2.14)$$

where: MXXSPDL = Number of fish lengths (FSIZE) covered in the horizontal direction per second at the fish's physiological horizontal maximum swimming speed

MXZSPDL = Number of fish lengths (FSIZE) covered in the vertical direction per second at the fish's physiological vertical maximum swimming speed.

The maximum physiological swimming speed is then decremented based on water quality conditions thought to slow swimming speed in blueback herring (e.g., Fay *et al.*, 1983). A simple linear function was used to decrement swimming performance under poor temperature and dissolved oxygen conditions. The physiological maximum swimming speed is first decremented if the fish is located in non-optimum water temperatures as:

$$U^t_{fish,MAX,dt} = U_{fish,MAX}*(1-|T^t(Z^t,X^t)-T_{opt}|/T_{opt}) \quad (2.15)$$

$$W^t_{fish,MAX,dt} = W_{fish,MAX}*(1-|T^t(Z^t,X^t)-T_{opt}|/T_{opt}) \quad (2.16)$$

where: $U^t_{fish,MAX,dt}$ = Temperature decremented maximum horizontal swimming speed (m/s)

$W^t_{fish,MAX,dt}$ = Temperature decremented maximum vertical swimming speed (m/s)

$T^t(Z^t,X^t)$ = Temperature (°C) at fish location (Z^t,X^t)

T_{opt} = Temperature (°C) for optimum blueback herring swimming performance.

Lastly, the maximum swimming speed is decremented when the fish is located in water with dissolved oxygen levels below a critical threshold (DO_{thres}). If the fish is located in water with dissolved oxygen levels above DO_{thres}, then the maximum swimming speed is not decremented for that time step. However, if dissolved oxygen levels are below the specified threshold, then the maximum swimming speed is decremented according to the following linear function:

$$U^t_{fish,MAX,dt,ddo} = U^t_{fish,MAX,dt}*(1-(DO_{thres}-DO^t(Z^t,X^t))/DO_{thres}) \quad (2.17)$$

$$W^t_{fish,MAX,dt,ddo} = W^t_{fish,MAX,dt}*(1-(DO_{thres}-DO^t(Z^t,X^t))/DO_{thres}) \quad (2.18)$$

where: $U^t_{fish,MAX,dt,ddo}$ = Maximum horizontal swimming speed (m/s) decremented for both temperature and dissolved oxygen conditions

$W^t_{fish,MAX,dt,ddo}$ = Maximum vertical swimming speed (m/s) decremented for both temperature and dissolved oxygen conditions

$DO^t(Z^t,X^t)$ = Dissolved oxygen (mg/L) at fish location

DO_{thres} = Dissolved oxygen threshold (mg/L), below which fish swimming performance suffers.

Within the algorithm, checks are placed to ensure swimming speed does not fall below zero. Volitional swimming in the longitudinal and vertical directions is then computed as the product of 'urgency to move' and 'maximum swimming speed'. Describing realistic movement behavior in the lateral direction is impossible since no variation or forcing functions exist in the lateral dimension. Instead, a random number is selected for 'urgency of movement' in the lateral direction and the maximum lateral fish swimming speed is arbitrarily set to 1. Component vectors of volitional swimming are computed as follows:

$$U^t_{fish} = U^t_{fish,MAX,dt,ddo} * X^t_{URGENCY} \quad (2.19)$$

$$W^t_{fish} = W^t_{fish,MAX,dt,ddo} * Z^t_{URGENCY} \quad (2.20)$$

2.3.1.5 *Step 5 – Simulating the hydrodynamics and water quality.*

The NFS can be run either coupled (i.e., integrated) with or decoupled (i.e., independently run) from the flow and water quality

model. Integrating the NFS into the physicochemical simulation model, as I have done, reduces computer disk storage requirements. Biological modeling convention suggests that a minimum of a thousand individuals be simulated to obtain statistically acceptable results when employing an individually-based model (IBM). The NFS emulates many characteristics of the IBM approach. For this reason, it is logical to use the same guidance for IBMs to select the number of individuals for the CEL Hybrid Ecological Model. For this project, approximately 10,000 virtual fish were simulated.

The CEL Hybrid Ecological Model simulations were performed on a Silicon Graphics (SGI) R12000 Octane workstation (~200MHz, 300 Mbytes RAM) with one simulation requiring about 6 CPU hours. An SGI Onyx workstation (4 R10000 processors) and an SGI PowerStation II (4 R10000 processors) were also utilized and were able to run approximately 12 independent simulations every 12 hours when all processors were available.

2.3.1.6 *Step 6 – Presenting model results.*

Engineering physicochemical simulation models typically require that biological data be converted into a Eulerian-based quantity, such as cell biomass, for integration into the model. On the other hand, the NFS simulates fish movement with sufficient realism that virtual fish created by the CEL Hybrid Ecological Model can be "sampled" using an algorithm that duplicates the scale and resolution of real-world sampling. This approach, i.e., virtual

sampling, enables the direct comparison of model results with actual field data without the need for conversion or reformatting of either of the data sets. The NFS for blueback herring in JST Lake was calibrated by comparing the distribution of virtual fish in the virtual system, created by the CEL Hybrid Ecological Model, to the distribution of actual blueback herring as estimated by dual-beam hydroacoustics.

A virtual gillnet was created as a plane extending from the virtual water surface to the bottom of the simulated system. Each time a virtual fish crossed the plane in either direction it was held in place on the 'net' and a counter incremented by one. Each virtual fish captured was tallied by depth so that the virtual catch could be summarized by depth and longitudinal distance. Similar logic was employed for virtual mobile hydroacoustic sampling, except that the plane was allowed to move within the virtual system at a speed similar to that of the sampling boat. However, virtual fish were not held in place after detection, and as in real hydroacoustic sampling, a fish could be counted more than once. As with virtual gillnetting, each virtual fish detected was tallied by depth so that virtual hydroacoustic survey data could be summarized by depth and longitudinal distance.

Virtual sampling results may be compared with actual field data in a number of ways. For instance, results from virtual hydroacoustic surveys may be compared with actual survey results by evaluating the differences between the virtual and actual fish

distributions, as detected by the surveys, along an axis of the water body (e.g., Figure 2.6) or by depth (e.g., Figure 2.7).

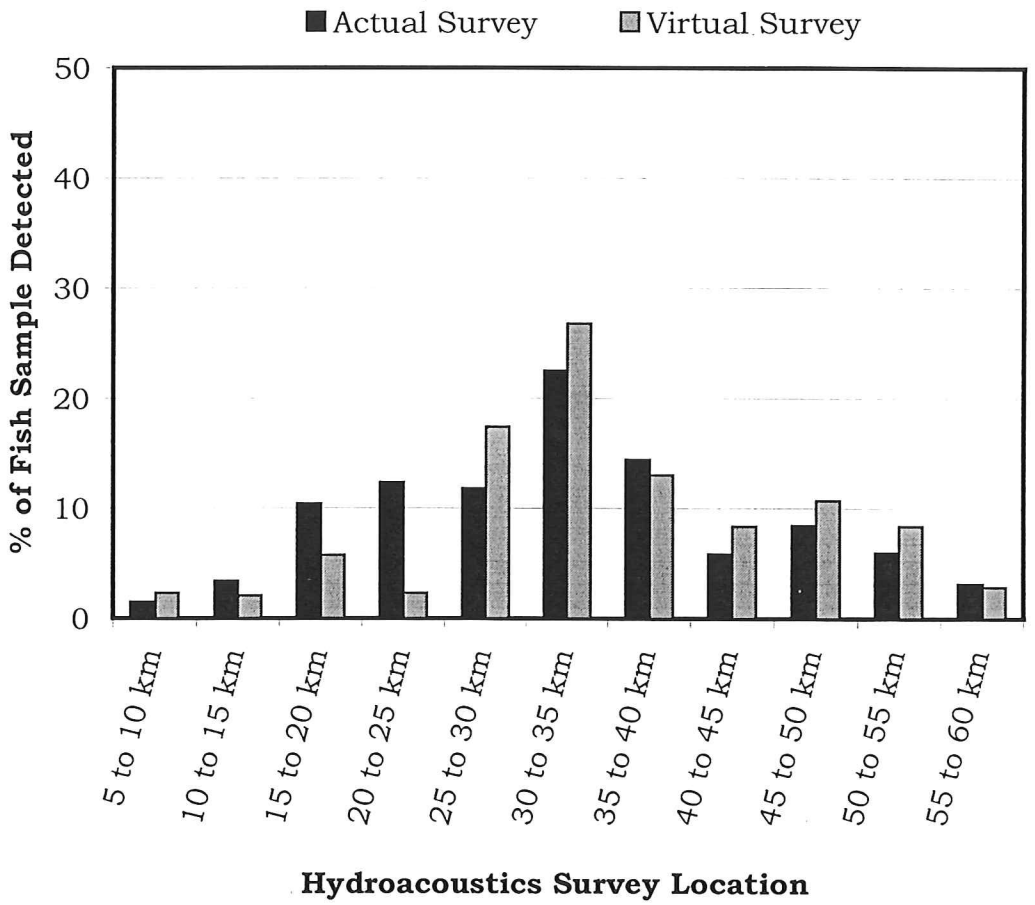
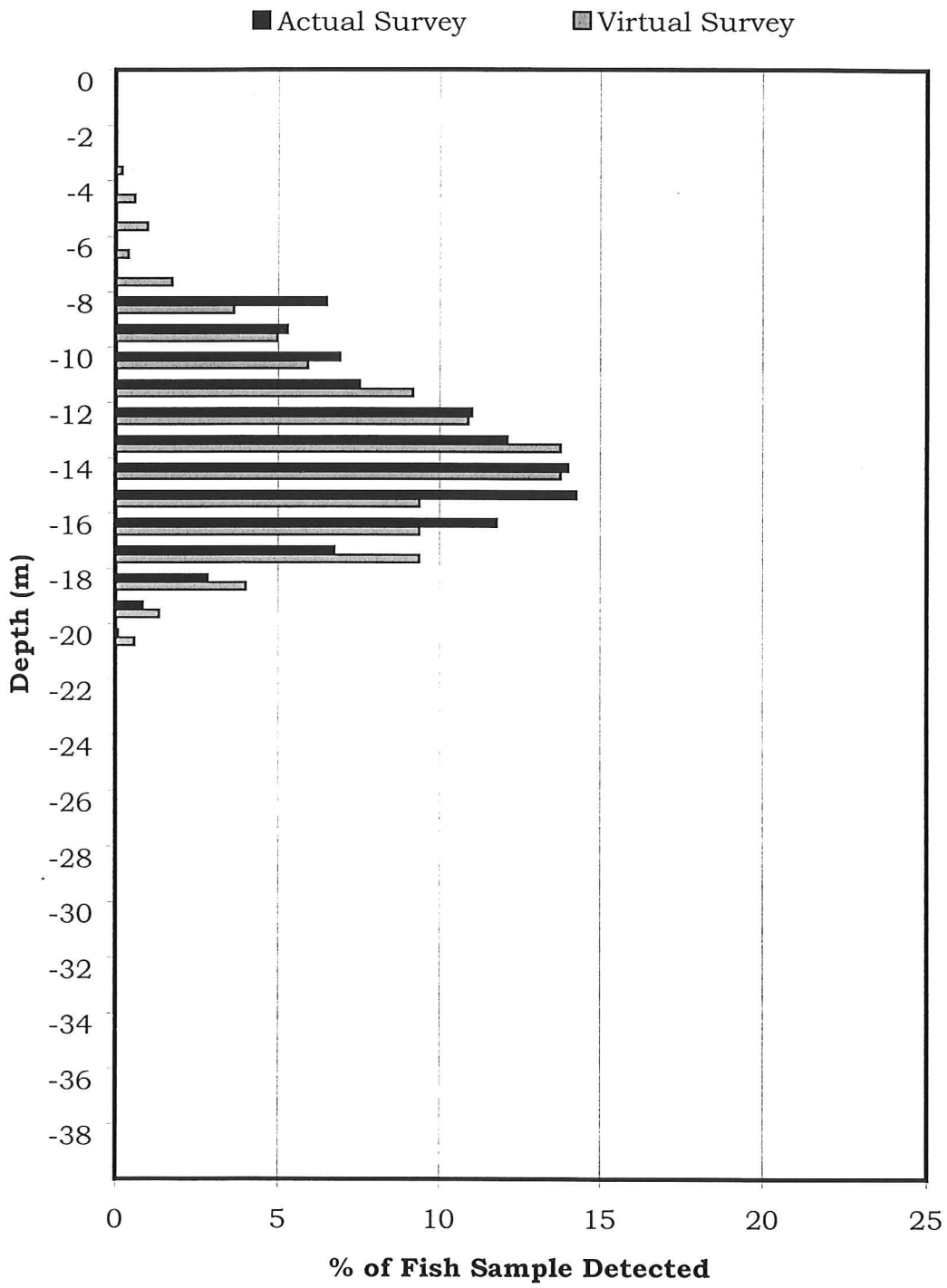


Figure 2.6 Example comparison between the longitudinal distributions of fish, as detected by actual and virtual hydroacoustic surveys.

Figure 2.7 Example comparison between the vertical distributions of fish, as detected by actual and virtual hydroacoustic surveys.


Actual Survey
Virtual Survey
0
-2
-4
-6
-8
-10
-12
-14
-16
-18
-20
-22
-24
-26
-28
-30
-32
-34
-36
-38
Depth (m)
0
5
10
15
20
25
% of Fish Sample Detected

2.4 **Discussion**

Depicting individuals of a biological population as 'particles' recognizes the duality that large, mobile organisms often exhibit. That is, they have some attributes best simulated using a Lagrangian modeling framework and other attributes best simulated using a Eulerian modeling framework. For example, the Lagrangian framework is ideal for simulating processes such as movement, reproduction, recruitment into the adult population, and mortality. The Eulerian framework is best suited for simulating physicochemical processes such as respiration and nutrient regeneration.

Simulating movement behavior is a fundamental step towards achieving a realistic simulation of aquatic ecosystems that include higher trophic level species. Once movement behavior can be captured, the Eulerian-Lagrangian couple can serve as a platform for the addition of bioenergetic processes such as species growth, mortality, and nutrient cycling as well as predator-prey interactions (e.g., Nonacs *et al.*, 1994; Schindler and Eby, 1997; Stockwell and Johnson, 1997) or any other relevant processes needed to elevate the model to an ecosystem perspective.

2.4.1 **Future Enhancement Opportunities**

Numerous opportunities exist for enhancing and modifying the CEL Hybrid Ecological Model and its biological module (the Numerical Fish Surrogate). Enhancements are all but necessary to

achieve more realistic simulations and predictions of movement behavior. Opportunities exist to apply CEL Hybrid Ecological Models to other higher and lower trophic level species.

The major limitation to fully implementing CEL Hybrid Ecological Models, in particular development of the biological module, is the lack of sufficient biological data. Suggested improvements that could enhance the NFS include:

- Model the physicochemical environment in all three dimensions.
- Enhance the logic used to compute a sensory ovoid and obtain gradients required to calculate urgency values.
- Enhance the stimuli-response rules. The rules were constructed so that future enhancements could be easily made whether through data mining of integrated engineering-biological data sets, optimization, more biological field data, better understanding of existing field data, or advancements in the understanding of fish sensory systems.
- Permit the "maximum response gradient" to change based on season of the year, time of day, or other important factors.
- Enhance the function for decrementing maximum fish swimming speed in non-optimum habitat conditions.
- Incorporate a schooling/dispersion algorithm for replicating predator-prey behavior known to dominate many species' movement behavior during the day.

- Incorporate turbulence, acoustics, and other variables of the flow and water quality fields that are believed to influence fish movement behavior.
- Use better techniques for locating optimum habitat within the sensory ovoid.
- Conduct a detailed analysis of the tradeoffs associated with using velocity values in place of velocity gradients for the purpose of computing urgency values.
- Enhance the logic used to normalize environmental variable gradient values, so cross-variable analysis can take place.
- Incorporate additional types of random movement or dispersion processes. Investigate the benefit of dispersing individuals in a population differently based on a behavioral state or other factors (Blackwell, 1997).

2.5 **Conclusion**

Coupled Eulerian-Lagrangian Hybrid (CEL Hybrid) Ecological Models provide the conceptual and computational bridge to unite existing engineering and biological modeling capabilities for improved ecosystem simulation. The couple, the Numerical Fish Surrogate, described in this chapter presents an opportunity to achieve realistic simulation of movement behavior of higher trophic level species. With the ability to simulate movement behavior, engineers and scientists can add, or further refine, existing models that describe other ecosystem processes.

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Simulating Mobile Populations in Aquatic Ecosystems Using a CEL Hybrid Ecological Model: Application and Evaluation

3.1 Abstract

Coupled Eulerian-Lagrangian Hybrid (CEL Hybrid) Ecological Models are a novel approach for simulating the population processes, particularly the movement dynamics, of higher trophic level species in aquatic environments. To demonstrate the potential and capabilities of CEL Hybrid Ecological Modeling, I developed and applied a model that simulates the movement behavior of blueback herring (*Alosa aestivalis*) in J. Strom Thurmond Lake, in a realistic context. The model was built by coupling a biological module (a Numerical Fish Surrogate) to an existing engineering flow and water quality model. Virtual sampling is introduced and used as a means to compare model output with actual field data.

Analysis of model results indicates the CEL Hybrid Ecological Model performed well in reproducing the distribution of blueback herring in the lake. Comparison of virtual and actual fish distributions, as obtained from virtual and actual hydroacoustic sampling, in the vertical plane yielded an r-squared value of 0.93 while comparison of virtual and actual distributions along the longitudinal axis of the lake produced an r-squared value of 0.67. I believe the results are good given the assumptions made and the inevitable shortcomings associated with development of a prototype.

3.2 **Introduction**

Hydraulic and water quality regimes of the aquatic environment are of principal importance in the evolution and maintenance of aquatic biota populations. Aquatic organisms are dependent on hydraulic forces for transport to necessary habitats as well as the advection of food sources to their location. Dissolved oxygen, temperature, nutrients, toxic substances, etc. (often grouped under the term 'water quality') are of principal importance in determining the rate and success of bioenergetic processes required for respiration, reproduction, recruitment, feeding, migration, and mortality.

3.2.1 **Previous Research**

With advances in computational resources and increased understanding of fish behavior have come numerous models attempting to capture the influence environmental and other factors have on fish movement behavior. While not mutually exclusive approaches, many models simulate either individual objects, representing from one to many actual individuals in a biological population, or the population as a whole, represented by some spatial, temporal, and/or probability distribution. For example, Sekine *et al.* (1997) developed a model to predict fish distributions based on water temperature, cover, current velocity, turbidity, food amount, depth, and stem of aquatic plants. However, weighted parameter values used to quantify the influence environmental

factors have on fish movement were calibrated in a lab, where fish swimming behavior may be markedly different from that in the field (Hughes and Kelly, 1996; Schilt and Norris, 1997). In addition, simulated movement was compared only with the general knowledge of fish behavior in flood situations.

Parrish and Turchin (1997) used an individually-based approach to identify sources of, and quantify the response to, various sources of attraction and repulsion within a fish school. Sources of attraction and repulsion were quantified in the context of some "congregation focus", i.e., a neighbor, a group of neighbors, or the entire fish school. A quantitative description of the rules describing individual movement was then developed by exploring the position and movement of individuals relative to other objects in the individual's environment, based on a balance of attractive and repulsive forces. However, individual movement was only explored as a response to 'objects' in its local; behavioral responses to environmental (physicochemical) conditions were not the focus of the research.

Other models include those developed by Laevastu and Larkins (1981), who used randomization, temperature, and food to simulate migratory fish movement and diffusion, and Zabel (1996), who used equations derived from diffusion equations and expressed as probability density functions to model the distribution of migrating juvenile salmonids. To date, although the importance of hydraulic forces and other environmental factors on the health of

aquatic populations is acknowledged and numerous tools are under development, few systematic approaches exist for analyzing and simulating the response of aquatic species to multiple visual, chemical, and mechanical factors (Tischendorf, 1997).

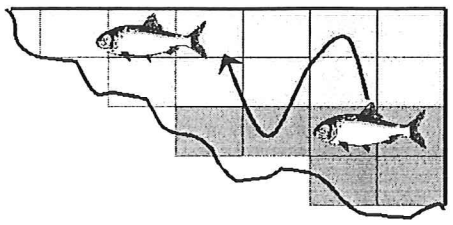
3.2.2 **CEL Hybrid Ecological Modeling**

The Coupled Eulerian-Lagrangian Hybrid (CEL Hybrid) Ecological Modeling System was developed (Chapter 1) to bridge the disconnect between existing physicochemical simulation and biological modeling traditions. The developed modeling system provides a framework for systematically analyzing the responses of biological organisms to multiple visual, chemical, and mechanical factors and also provides a framework for the realistic replication, or simulation, of such movement responses. The name of the modeling system is derived from the mathematical process used to integrate the simulation of animal movement into existing physicochemical simulation models.

Physicochemical models, often employed by engineers to simulate the hydraulics and chemical regimes of aquatic systems, use the Eulerian framework to solve established equations of flow and water quality. This framework involves representing the aquatic system as a series of compartments, fixed in space, through which fluxes of mass and energy are routed and balanced. On the other hand, spatiotemporal population models, often employed by biologists to simulate animal movement, most often use the

Lagrangian framework to solve equations for position in space and time. The Lagrangian framework is centered on individual objects, rather than on a point fixed in space, and is, therefore, not stationary (Turchin, 1997). This framework allows the modeler to track the exact spatial coordinates of each individual, which increases the compatibility with tracking data and analytical treatments of movement processes (Tischendorf, 1997).

In order to integrate Lagrangian-based movement models, or Lagrangian movement, into Eulerian-based physicochemical simulation models, an individual, a group of individuals, or an entire population is symbolically represented as a single particle, or point, in space (Matuda *et al.*, 1993). A particle-tracking algorithm can then be used to move the 'particle' continuously within and between compartments (e.g., grid cells for 2-D models) that comprise the system (Figure 3.1).



= **Symbolic Population**

Figure 3.1 Placing a virtual organism in an engineering flow and water quality model. The Eulerian-based engineering (physicochemical) model represents and simulates spatial heterogeneity through the use of multiple compartments, each compartment representing an environment in which all conditions have been averaged (i.e., spatially integrated). A particle-tracking algorithm may be used to move a 'particle', or virtual fish, within and between compartments comprising the system.

Recognizing that movement decisions of an individual fish can be viewed as a balance of forces (Okubo, 1980), in particular, a set of attractions to and repulsions from various sources or foci (Parrish and Turchin, 1997), behavioral cues, or stimuli-response rules, can be programmed into the particle-tracking algorithm to emulate the fish's movement behavior. Enhancement of the particle-tracking algorithm through the addition of stimuli-response rules, which when taken as a whole dictate the pattern of movement (Schilt and Norris, 1997), creates a virtual fish capable of making individual movement decisions related to the spatial information as provided

by the Eulerian-based model (Tischendorf, 1997) in a way that emulates the behavior of real fish.

Specifically, stimuli-response rules are used to determine the speed and direction of volitional swimming. These rules are developed based on Niche theory and couched as a Markov Chain behavioral model (Haccou and Meelis, 1992). Niche theory tells us that biological species have ecological "preferences," meaning that they are found in areas where environmental variables have some "optimal" value (Legendre *et al.*, 1997). Appropriate environmental variables to use in developing the stimuli-response rules can be obtained from a variety of sources, including published literature, field data, and field experience.

These stimuli-response rules transform the 'passive' object into a virtual organism by allowing the object to make decisions regarding volitional movement based on any number of physicochemical and other factors (Matuda *et al.*, 1993; Tischendorf, 1997). Couching the stimuli-response rules as a Markov Chain statistical model allows the object to make decisions based on any number of factors, including the time of day, season of the year, food availability, local predators or prey, etc. These enhanced particle-tracking 'rules' constitute the biological module of the CEL Hybrid Ecological Model.

3.3 CEL Hybrid Ecological Model Application

To create the CEL Hybrid Ecological Model, a biological module (the Numerical Fish Surrogate, Chapter 2) is coupled to an existing engineering flow and water quality model. The CEL Hybrid Ecological Model was developed to realistically simulate the movement behavior of blueback herring (*Alosa aestivalis*), a cool water fish, in J. Strom Thurmond Lake for the summer of 1996. Although the model is capable of using any number of physicochemical and other environmental factors to elicit emergent fish behavior, only water velocity, temperature, and dissolved oxygen were used. Virtual sampling was used as the means to compare model output with actual field data.

3.3.1 Engineering Model

Hydrodynamic and water quality processes in the lake were simulated using an existing engineering model. The model, CE-QUAL-W2 Version 3.0 (Cole and Tillman, in prep), is a two-dimensional, laterally-averaged, dynamically-linked hydrodynamic and water quality model. CE-QUAL-W2 has been under continuous development since the mid-1970s and has been applied to numerous lakes, estuaries, rivers, pit lakes, and reservoirs, including over 14 reservoirs in the southeastern United States alone (e.g., Cole and Tillman, 1996).

A laterally-averaged model, CE-QUAL-W2 does not compute flow or water quality variations in the lateral direction. Since no

variation exists to elicit movement behavior, movement in the lateral direction is simply random (see Figure 3.2). Movement in the lateral direction, albeit random, allows virtual fish to swim upstream into tributaries by way of a bookkeeping scheme developed specifically for the Numerical Fish Surrogate (NFS) module. Movement into downstream tributaries is also permitted, using existing mechanics within CE-QUAL-W2.

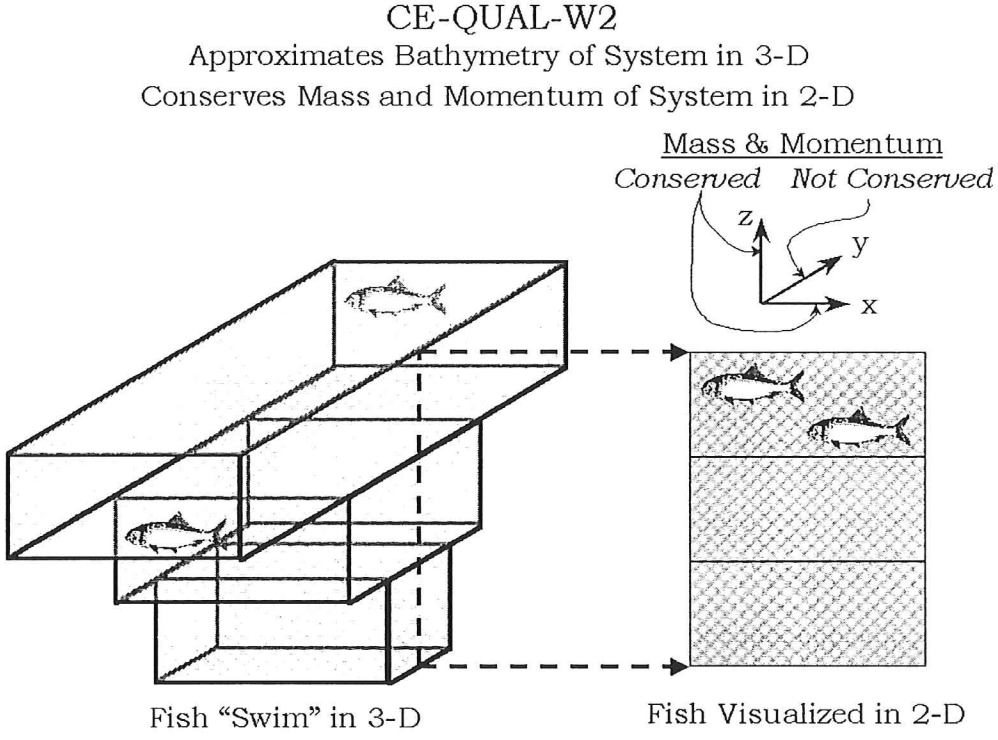


Figure 3.2 Lateral movement in a laterally-averaged flow and water quality model. Although movement is random, the movement enhances the realism of the simulation and also allows the virtual fish to swim upstream into tributaries.

3.3.1.1 *Site Characteristics*

The hydrosystem studied consisted of three dams and two reservoirs on the Savannah River between Georgia and South Carolina. Hartwell Dam defines the upstream boundary for Richard B. Russell (RBR) Lake and the downstream boundary of this reservoir is Richard B. Russell (RBR) Dam. Releases from RBR Dam flow into the headwaters of J. Strom Thurmond (JST) Lake; RBR Dam was operated as a pump-storage project from March 1996 to October 1996 with maximum conventional releases of 518 m^3/s (60,000 ft^3/s) and maximum pumpback of 259 m^3/s (30,000 ft^3/s). The downstream boundary of JST Lake is Clarks Hill Dam. Although fish movement is simulated only in the downstream reservoir (JST Lake, Figure 3.3), the entire hydrosystem is modeled by CE-QUAL-W2 since the water quality of JST Lake is heavily influenced by the conditions in RBR Lake near RBR Dam (Cole and Tillman, in prep).

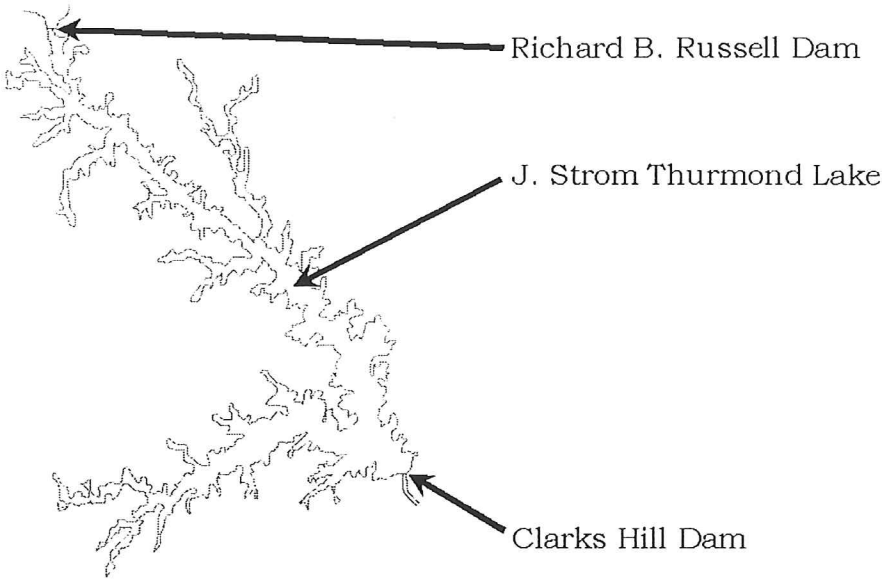


Figure 3.3 J. Strom Thurmond (JST) Lake: surface area = 28,320 ha; total length = 61 km. JST Lake resides along the Savannah River between South Carolina and Georgia in between Richard B. Russell and Clarks Hill Dams.

Releases from RBR Dam impact more than just the flow and water quality regimes in the tailrace. Blueback herring populations are also impacted. Well oxygenated cool water discharges from RBR Dam, and warm stratified conditions throughout JST Lake in August thru October, help to concentrate blueback herring in the tailrace of RBR Dam (Isely, 1996). During pumpback, blueback herring can dominate entrainment and have become a serious problem for continued pumpback operation. Rapid changes in water temperatures may also impact the timing of blueback herring spawning (Meador *et al.*, 1984). The impact RBR Dam has on the flow and water quality regimes of JST Lake and on the blueback

herring population, through both direct (i.e., entrainment) and indirect (i.e., the creation of desirable habitat in the tailrace where entrainment is possible) means, makes JST Lake an ideal site for implementing the CEL Hybrid Ecological Modeling System.

3.3.2 **Biological Data**

The simulation and analysis of blueback herring movement behavior was selected not only because of the entrainment issue at RBR Dam, but also because the environmental factors determining optimal habitat for blueback herring are relatively well-known. Research literature on blueback herring (e.g., Isely, 1996; Thomas *et al.*, 1992; Osteen *et al.*, 1989; West *et al.*, 1988; Dadswell, 1985; Meador *et al.*, 1984; Fay *et al.*, 1983; Pardue, 1983; Skjeveland, 1982; Loesch and Lund, 1977) suggests that moderate water temperatures (e.g., 14°C-27°C), dissolved oxygen, and fast-flowing water are important factors that attract blueback herring, particularly for spawning. Other research (e.g., Ploskey *et al.*, 1994) has even focused on the behavioral responses of blueback herring to various specific stimuli. In 1996, hydroacoustic and gillnet surveys (Dennerline and Degan, in prep) were performed to gain insight into the location, movement, behavior, and habitat preferences of blueback herring in JST Lake. The gillnet and hydroacoustic survey results from August 1996 were used to calibrate the NFS.

The locations of blueback herring over time were determined by integrating the results from dual-beam hydroacoustics and

vertical gillnets. Vertical gillnets were used to estimate the species composition of targets detected by the hydroacoustics versus depth. Vertical gillnets were composed of two mesh panels, each 6 feet wide. Gillnets were placed at several stations. At each station, net repetitions were used to increase the statistical rigor of the survey results. Net repetitions consisted of 3 nets with mesh panel combinations of ($^3/_8$", $^1/_2$"), ($^5/_8$", $^3/_4$"), and ($^7/_8$", 1").

Dual-beam hydroacoustic surveys were conducted on the reservoir over a period of three non-contiguous days. The main stem of JST Lake was surveyed by hydroacoustics in a series of lateral transects, each one upstream of the previous. These surveys were conducted at night, starting in the evenings of August 14th (JDAY 227), August 21st (JDAY 234), and August 23rd (JDAY 236).

To incorporate the hydroacoustic results into the CEL Hybrid Ecological Model, for which all lateral process are averaged (i.e., no lateral information), results were grouped into 5 km longitudinal segments beginning at the upstream end of the reservoir (i.e., at RBR Dam). Organizing data in this manner permitted the calculation of variability in the hydroacoustic results for each segment. No hydroacoustic sampling was conducted in the upstream-most 5 km segment near RBR Dam.

3.3.3 **Modeling Procedure**

Numerous methods can be used to calibrate the stimuli-response rules that make up the NFS. Some of the methods I used

were qualitative in nature and used, with intuition, as a first-cut in parameterizing the stimuli-response rules. Other methods were quantitative in nature and used to fine-tune the parameters of the stimuli-response algorithm. Both types of methods were of benefit in the calibration process. I believe that intuition is a significant resource, when used appropriately, and should not be discounted. Currently, not enough is known about higher trophic level aquatic species to disallow intuitive estimates of how their behavior is structured.

The first step in calibrating the NFS involved developing preliminary stimuli-response rules capable of emulating fish movement behavior under well-behaved flow and water quality conditions, where fish movement can be fairly well judged. After these preliminary rules were developed, the rules were incorporated into the hydrodynamic and water quality module of the CEL Hybrid Ecological Model. The CEL Hybrid Ecological Model was then programmed to output instantaneous movement decisions made by the population at each time step as well as to track the decision-making history of the population over the course of the simulation. These instantaneous and cumulative values were then used to evaluate the realism of the movement behavior. These decision histories allowed insight into whether fish were responding too often or too seldomly to particular components of the flow and water quality fields. Decision histories provided the means necessary to fully calibrate many of the parameters. However, several

parameters, particularly variables influencing the response to horizontal velocities and the amount of horizontal random movement, proved especially difficult to calibrate because of synergistic interactions. To overcome the difficulty, a multi-dimensional matrix was created consisting of values that I believed bracketed the optimum parameter values. Successive application of these matrices to areas where previous matrices indicated good simulation results enabled the final calibration of even the most difficult and synergistically-behaving variables.

3.3.3.1 *Virtual Sampling*

The importance of outputting model results in a manner consistent with the scale and resolution of field data for the purpose of calibrating a biological model should not be underestimated. In the past, Eulerian-based models required that biological items be converted into a format consistent with other variables handled by the model. Typically, this involved converting biota into biomass or some other compartment-averaged value. However, field surveys are inherently variable, influenced by factors such as the natural patchiness of population distributions, fish behavior, boat and gear types and operational methods, and survey design and environmental conditions (Jessop, 1985). The conversion of such field data into compartment-averaged values almost assuredly degrades the integrity of the field data and its compatibility with analytical treatments of movement behavior. To maintain the

integrity of the field data and ensure its compatibility with the NFS model, virtual sampling was developed to produce model results that are directly comparable to actual field data.

The process of virtual sampling entails programming the NFS so the hydrodynamic and water quality environment created by the physicochemical simulation model, within which the virtual fish are located, may be sampled with gear such as virtual gillnets or virtual hydroacoustic beams. Virtual sampling within the CEL Hybrid Ecological Model can be structured such that virtual counterparts to the actual activity have the same capabilities and liabilities and can be deployed using the same, or very similar, survey designs and operational methods. This enables the direct comparison of model output with results from field surveys.

In the virtual ecosystem created by the CEL Hybrid Ecological Model, virtual gillnets can be created with sizes and selectivities comparable to those of gillnets used in actual sampling. Virtual hydroacoustic sampling can be achieved by creating an elliptical cone equivalent in size, range, and characteristics to the hydroacoustic beam used in actual sampling.

3.3.3.2 *Movement Visualization*

In addition to virtual sampling, movement visualization software (Figure 3.4) was developed to assist with calibration. The software displays fish movement in a user-friendly format along with selected characteristics of the flow and water quality environment

(i.e., water temperature and dissolved oxygen concentration). Visualization helped to determine whether virtual fish were responding to habitat conditions, on a macro scale, in a realistic manner.

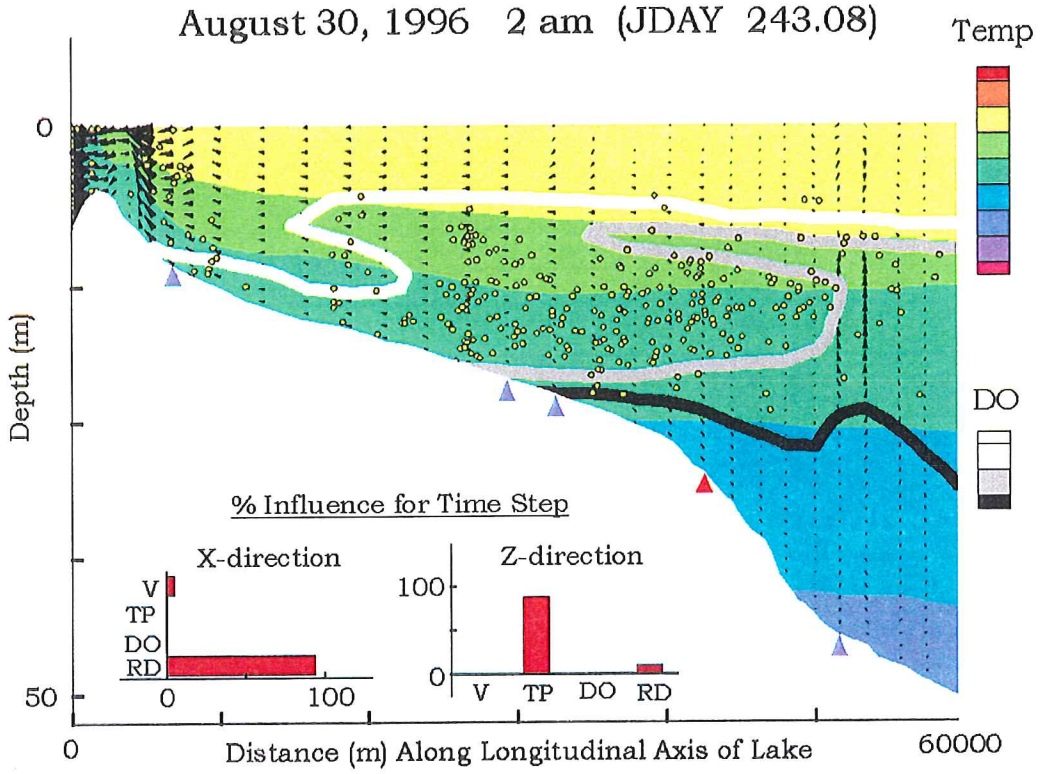


Figure 3.4 Visualization software developed for the CEL Hybrid Ecological Model. Yellow dots represent virtual fish; colored contour fills represent water temperature; gray-scaled contour lines represent selected dissolved oxygen concentrations; black arrows represent velocity vectors; red bar charts indicate instantaneous fish responses to various environmental factors for each movement direction; blue triangles indicate an intersecting tributary; and red triangles indicate a drastic change in reservoir cross-sectional area.

3.4 **Model Performance**

Graphical and statistical analyses of the CEL Hybrid Ecological Model's performance in simulating the movement behavior of blueback herring suggest the model is capable of simulating aquatic species movement, even in dynamic physicochemical environments. This ability can contribute to the discussion of conceivable consequences that modified physicochemical environments have on the movement, and health, of biological species (Tischendorf, 1997). Analysis of the virtual sampling results reveals a general agreement between the observed and predicted fish distributions in both the longitudinal and vertical planes. This is particularly encouraging in light of the assumptions required to construct the NFS and the variability of the actual field data.

Distributions of blueback herring, as obtained from actual and virtual hydroacoustic surveys, were compared in the longitudinal and vertical directions using both graphical and statistical means. For statistical comparison of the distributions, I selected the coefficient of determination. The coefficient of determination, or r-squared value, roughly indicates the amount of total variation in the actual data that can be explained by the CEL Hybrid Ecological Model.

3.4.1 **Vertical Distribution**

The vertical distribution of fish within a managed water body is important to the biologist and the water resources manager alike since the operation of dams and reservoirs can impact the vertical stratification of lakes. Alterations in stratification patterns may change the prey stratification and the spatial/temporal overlap with predators as well as constrain the distribution of fish and possibly reduce the access to zooplankton resources important to planktivorous fishes such as blueback herring (Stockwell and Johnson, 1997). Therefore, any model hoping to capture the impact dam and reservoir operations have on biological populations must first be able to reproduce the vertical distribution of those species under previous known conditions.

Figure 3.5 shows the actual and virtual blueback herring distributions in the vertical direction for the entire length of JST Lake. Results from gillnet surveys indicated that a majority of the hydroacoustic targets below the thermocline (approximately 8m below the water surface during hydroacoustic sampling) could be assumed to be blueback herring. Gillnet surveys provided inconclusive results on the species composition of the targets above the thermocline. Since it was not possible to determine the proportion of blueback herring above the thermocline accurately, hydroacoustic targets above the thermocline were not used. Statistical comparison of the actual and virtual distributions in the vertical direction yielded an r-squared value of 0.93.

Figure 3.5 The vertical distribution of the entire JST Lake blueback herring population as detected by actual and virtual hydroacoustic surveys.

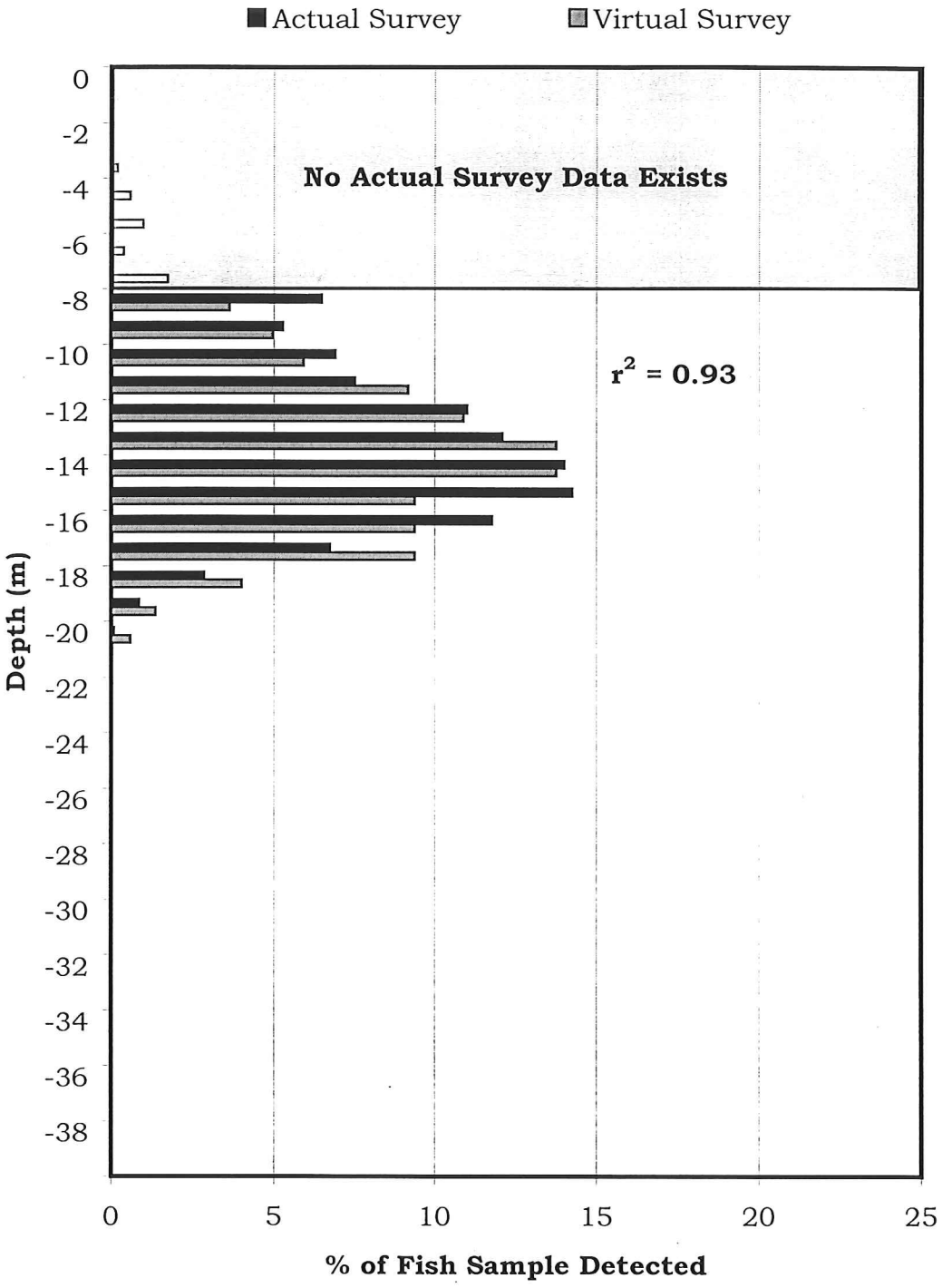

Actual Survey
Virtual Survey
No Actual Survey Data Exists
r^2 = 0.93
Depth (m)
0
-2
-4
-6
-8
-10
-12
-14
-16
-18
-20
-22
-24
-26
-28
-30
-32
-34
-36
-38
0
5
10
15
20
25
% of Fish Sample Detected

Figure 3.6 shows the cumulative distribution function (CDF) of the entire blueback herring population in JST Lake in the vertical direction. From the cumulative distribution function, it can be seen the two distributions are very similar with the main discrepancies occurring at the tails of the vertical distribution. The discrepancy at the tail nearer the water surface is almost assuredly attributable to the absence of actual field data above the thermocline.

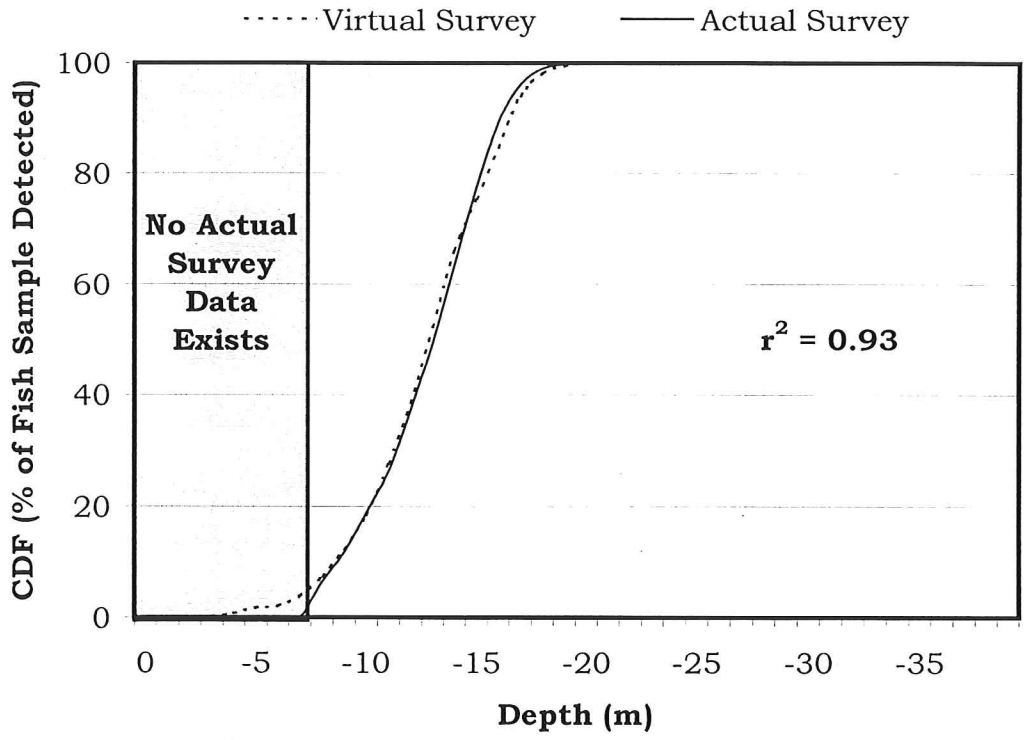


Figure 3.6 Cumulative distribution function (CDF) of the vertical distribution of the entire JST Lake blueback herring population as detected by actual and virtual hydroacoustic surveys.

3.4.2 **Longitudinal Distribution**

The longitudinal distribution of species within a managed water body is important because the operation of dams and reservoirs impacts certain areas of the water body more than others. The location of species is important in determining whether management will impact the population. Hence, any model hoping to capture the impact dam and reservoir management may have on biological populations must first be able to locate where the populations will be under known conditions.

In JST Lake, Figure 3.7 shows the longitudinal distribution of blueback herring in 5 km segments, except for near RBR Dam where no hydroacoustic surveys were conducted. Survey results indicate the CEL Hybrid Ecological Model performed well in reproducing the longitudinal distribution of blueback herring. Statistical comparison of the actual and virtual longitudinal distributions yielded an r-squared value of 0.67.

Figure 3.8 shows the CDFs for blueback herring in the longitudinal direction. From the CDFs, it can be seen the plots are quite similar indicating little difference between the modeled and actual distributions, as detected by virtual and actual hydroacoustic surveys, respectively. The main discrepancy occurs, approximately, $^1/_3$ the length of the reservoir downstream from RBR Dam. I believe this discrepancy is caused by virtual fish 'unwilling' to leave the nearby high velocity area just downstream. This proves to be an opportunity for future improvement in the NFS.

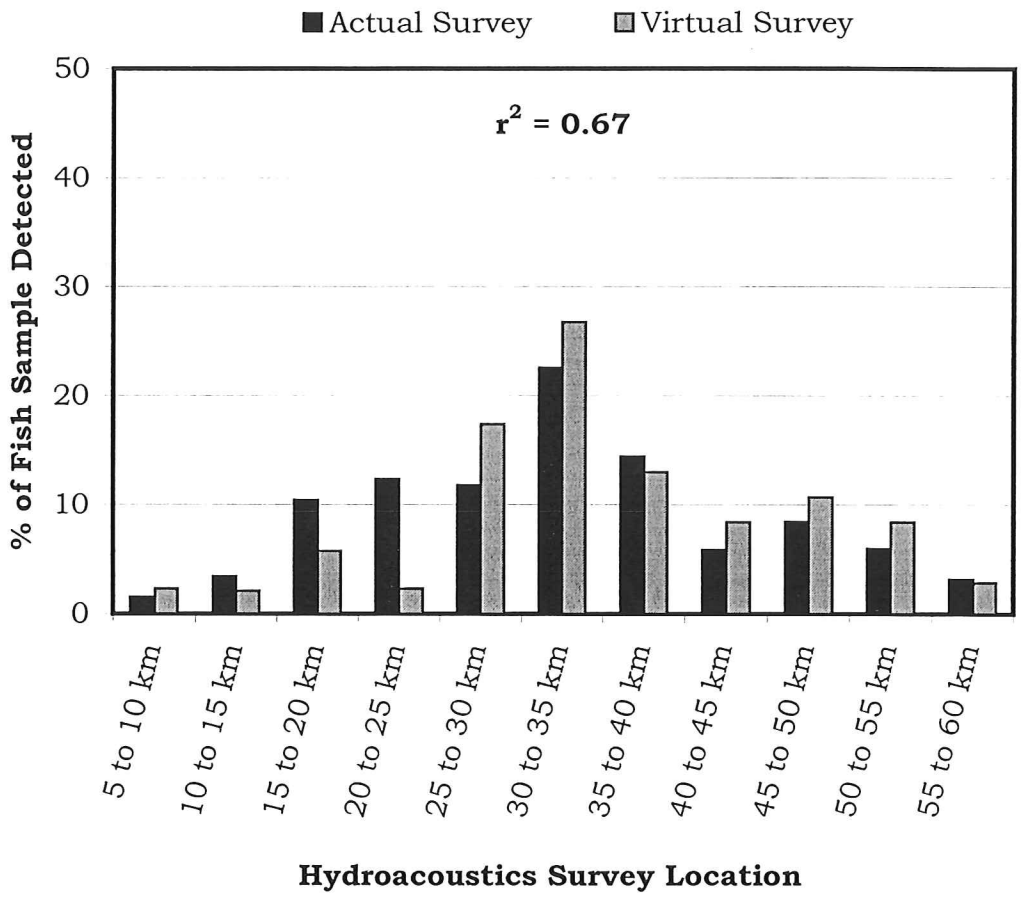


Figure 3.7 The longitudinal distribution of the entire JST Lake blueback herring population, except for the upstream-most 5km segment where no surveys were conducted, as detected by actual and virtual hydroacoustics.

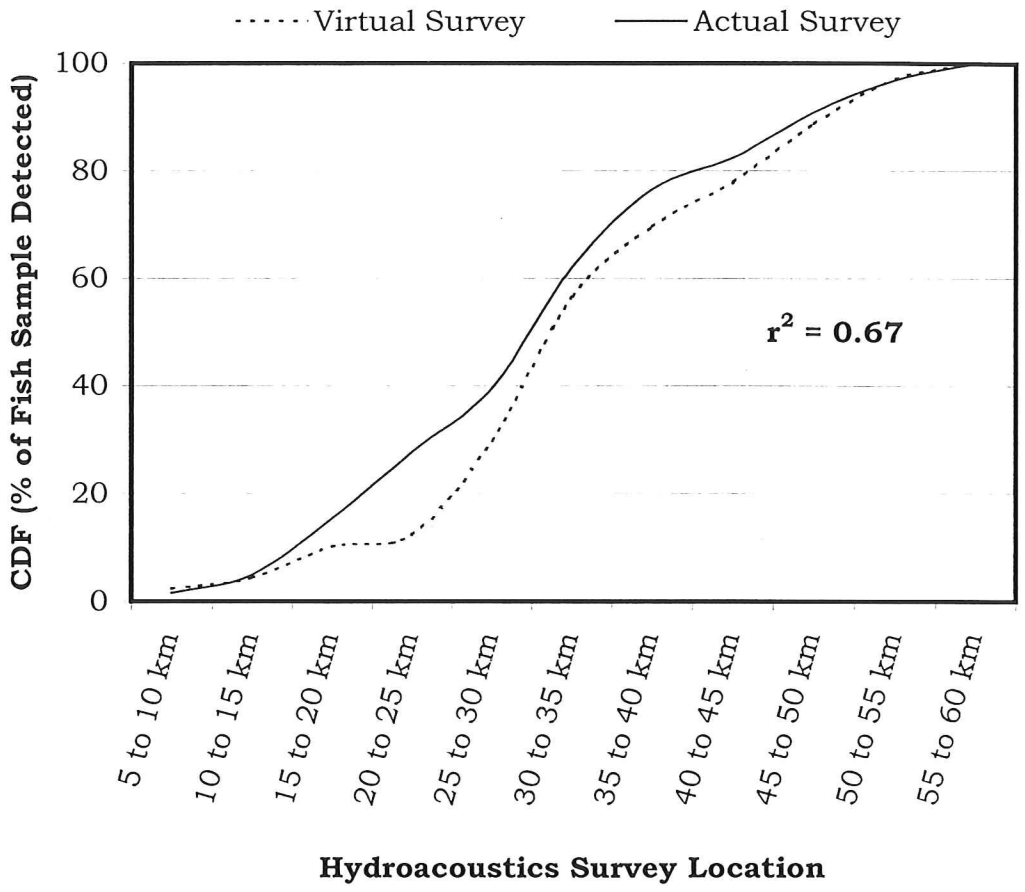
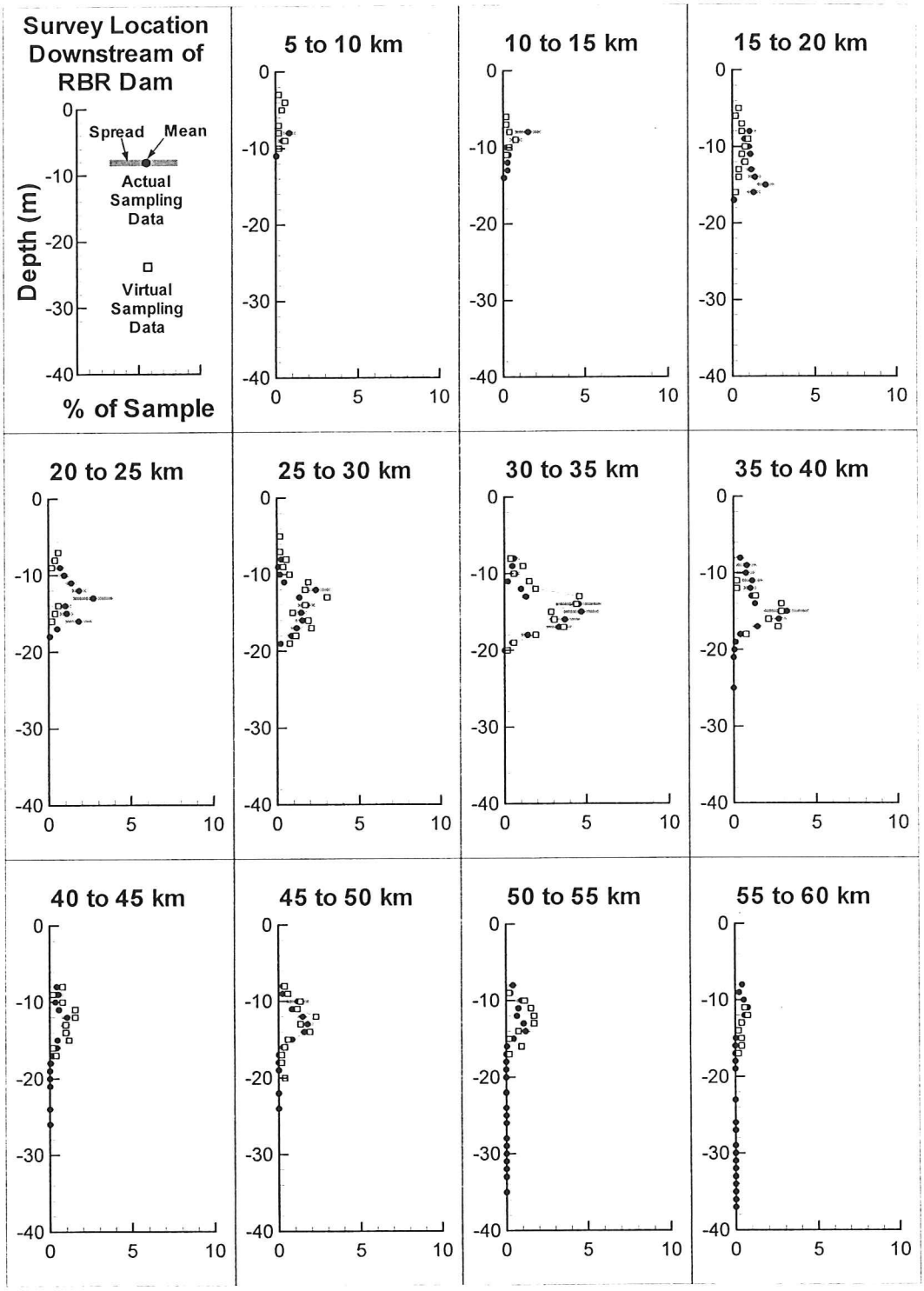


Figure 3.8 Cumulative distribution function (CDF) of the longitudinal distribution of the entire JST Lake blueback herring population, except for the upstream-most 5km segment where no surveys were conducted, as detected by actual and virtual hydroacoustics.

3.4.3 **Vertical Distribution by Longitudinal Segment**

Figure 3.9 shows the vertical distribution of virtual blueback herring in each 5km longitudinal segment. As indicated in Figures 3.7 and 3.8, the model seems to perform quite well in all areas, with the exception of one or two segments (i.e., 15 to 20 km and 20 to 25 km segments downstream from RBR Dam). In all other segments, the model performed quite well in placing virtual blueback herring in the correct proportion both longitudinally and vertically within the virtual reservoir.

Figure 3.9 Vertical distribution by longitudinal segment of the blueback herring population in JST Lake, as detected by actual and virtual hydroacoustic surveys. "Spread" of the actual data is equal to ¼ the standard deviation of the survey results.


Survey Location Downstream of RBR Dam
Depth (m)
Spread
Mean
Actual Sampling Data
Virtual Sampling Data
% of Sample
5 to 10 km
10 to 15 km
15 to 20 km
20 to 25 km
25 to 30 km
30 to 35 km
35 to 40 km
40 to 45 km
45 to 50 km
50 to 55 km
55 to 60 km

3.4.4 **Decision-Making Histories**

The NFS tracks the decisions made by every virtual fish during simulation. A summary of the decisions is output in the form of instantaneous and cumulative decision histories. These histories can be compared with intuitive estimates of how individuals should, or are likely to, respond. For instance, a decision history showing virtual blueback herring responding to temperature gradients in anoxic zones may be realistic (this behavior has been observed in JST Lake), while a decision history showing virtual fish responding to dissolved oxygen gradients in water temperatures greater than 30°C may indicate an err in the model since blueback herring, a cool water species, would likely swim towards cooler temperatures first, rather than respond to dissolved oxygen gradients.

The decision histories for the best simulation mostly confirmed my intuitive guesses as to the forcing functions behind blueback herring movement behavior. Decision histories revealed that for the best parameter set (yielding best simulation results) horizontal velocity was the dominant physicochemical stimulus in eliciting longitudinal movement. For vertical movement, temperature was the dominant physicochemical stimulus. Interestingly, however, randomization dominated all of the physicochemical stimuli in determining movement. These results, however, may be somewhat realistic; Tischendorf (1997) noted that the movement of organisms lies somewhere between random walk

and straight movement paths. For blueback herring, it's possible that they are attracted to particular stimuli and once this stimulus is arrived at random movement ensues, until a new stimulus becomes the focus of movement.

Table 3.1 shows the cumulative decision history for individuals in the virtual blueback herring population for the best simulation. Table 3.1 tabulates the influences behind all movement decisions. Movement decisions are attributable to either a stimulus response or randomization.

Table 3.1 Cumulative Decision History of Virtual Population.

Physicochemical Stimulus or Randomization	Longitudinal Movement Decisions (%)	Vertical Movement Decisions (%)
Horizontal Velocity	42.7	3.8
Vertical Velocity	0.0	1.1
Temperature	0.0	45.0
Dissolved Oxygen	0.0	6.0
Randomization	57.3	44.2

The dominance of horizontal velocity over vertical velocity, temperature, and dissolved oxygen in the longitudinal direction is intuitive since these other stimuli vary negligibly in the horizontal plane. Stratification patterns within a confined water body, such as

a reservoir like JST Lake, tend to be strong in the vertical direction and very weak in the horizontal direction since the patterns are heavily influenced by air temperature and wind at the water surface. The dominance of horizontal velocity was so strong, in fact, that even when vertical velocity, temperature, and dissolved oxygen were disproportionately weighted virtual fish would still respond to horizontal velocity.

In the vertical direction, temperature was the dominant stimulus in eliciting fish movement. Again, the strong stratification pattern in the vertical direction is probably responsible for this outcome. Although temperature was singled out as the dominant stimulus, dissolved oxygen and temperature stratification patterns are usually heavily correlated in managed reservoirs such as JST Lake. For this reason, it's imaginable that scenarios exist where equally good simulation results can be obtained where dissolved oxygen plays a much larger role in eliciting vertical movement. For the most part, both horizontal and vertical velocities varied little in the vertical direction, which probably explains their lack of influence in eliciting vertical movement.

3.4.5 **Sensitivity Analysis**

Sensitivity analyses were performed on the model to gage its sensitivity to selected input parameters and randomization. Input parameters selected for the sensitivity analyses included: number of fish, fish release location, fish release date, time step of the NFS,

and stimuli weights. In addition, since the NFS contains stochastic components, a sensitivity analysis was performed to determine the influence different randomization would have on the best simulation results. Among other things, analysis of the NFS's random component yielded a distribution of model results for the best parameter set.

Table 3.2 summarizes the results of the sensitivity analyses. Graphical results, analogous to Figures 3.5 through 3.8, are presented for the sensitivity analyses simulations in Appendix D.

Table 3.2 Sensitivity Analyses Results.

	R-squared Values	
Simulation	Longitudinal Distribution	Vertical Distribution
Best:	0.67	0.93
• Number of Fish: 8960		
• Released: Uniformly		
• Released: May 1, 1996		
• Time Step: 9 minutes		
Number of Fish:		
• 5600	0.57	0.88
• 11,200	0.62	0.90
Release Location:		
• Upstream	0.58	0.92
• Mid-Lake	0.52	0.92
Release Date:		
• March 31, 1996	0.61	0.95
• June 1, 1996	0.57	0.91
Time Step:		
• 5 minutes	0.48	0.92
• 15 minutes	0.59	0.89
Stimuli/Parameter Weights:		
• Horiz Velocity (+20%)	0.70	0.94
• Temperature (-30%)	0.61	0.91
• Dissolved Oxygen (-30%)	0.52	0.82
• Randomization (-30%)	0.40	0.75

3.4.5.1 *Best Simulation*

The parameter set yielding the best simulation results is listed in Appendix C. To simulate the large blueback herring population in JST Lake, 8960 virtual fish were released uniformly throughout the virtual reservoir in both the longitudinal and vertical directions on May 1, 1996. Both the number of virtual fish used and the release date were selected at the outset of calibration based on a preliminary understanding of the model's performance. Although sensitivity analyses proved otherwise, at the outset of calibration it was thought using fewer fish in such a large virtual system or releasing fish closer to the August survey dates would result in less than reliable results.

The flow and water quality module of the CEL Hybrid Ecological Model (CE-QUAL-W2) runs at time steps averaging 1.5 minutes. During calibration, it was observed that better vertical and longitudinal fish distributions resulted when the NFS (which can run at time steps greater than that of the flow and water quality model) operated at time steps averaging 9 minutes.

Although the parameter set in Appendix C shows the parameter values used to obtain the best simulation, variability is to be expected since stochastic processes are used in several portions of the NFS. Section 3.4.5.6 discusses the variability of model results associated with the best parameter set.

3.4.5.2 *Varying the Number of Fish*

Analysis investigating whether the number of virtual fish used influences model results showed that for the population size range tested no significant difference in model results was evident. However, during NFS development and calibration it became apparent that a threshold does exist below which model results become increasingly unstable and unreliable. As the number of virtual fish used increased, particularly above 1000, model results appeared stable. Given the size of the virtual system, it seems reasonable to conclude that virtual populations of less than 1000 individuals may allow pockets of individuals to influence model results out of sync with reality.

3.4.5.3 *Varying Fish Release Date & Location*

As anticipated, neither the location nor the date of release of the virtual fish population greatly influenced model results. This would seem to indicate an inherent stability and robustness about the model as the algorithms have proved to be adapt at accounting for varying inputs that we know should not influence model performance or results. On the same token, however, there is certainly a limit to how far the model can be pushed. For instance, releasing fish just days or hours before the hydroacoustic surveys are conducted may not give the virtual population enough time to disperse and reach some sort of dynamic equilibrium.

3.4.5.4 *Varying the Time Step of the NFS*

Although not explicit in the sensitivity analysis, during NFS development and calibration it became apparent that shorter time steps, on average, produced better vertical distributions of virtual fish (r-squared values ≥ 0.98) and much longer time steps, on average, produced inferior distributions (r-squared values ≤ 0.40). The reason for this model behavior may also help describe the apparent ineffectiveness in using the time step to manipulate longitudinal population dispersion (discussed later). In the vertical direction where distances are much shorter, doubling the time step can significantly increase the number and magnitude of overshoots. Gradients in the vertical direction are quite strong compared to those in the longitudinal plane, and this results in an ability in virtual fish to find optimal habitat in the water column with relative ease since gradients, which are used to make decisions regarding movement, are readily noticeable. Since virtual fish can rely heavily upon these vertical gradients to find optimal positions in the water column, overshoots tend to disturb rather than enhance the search for optimal habitat in the water column.

On the other hand, gradients in the longitudinal plane are quite weak and even though this can be compensated for in the model, areas of optimum habitat may be long distances from one another and may not be within the detectability of the virtual fish. For this reason, overshoots may enhance the search for optimum habitat in the longitudinal direction since overshoots may cause fish

to end up in areas near optimum habitat where they otherwise would not have moved. The sensitivity analysis indicates a decrease in longitudinal r-squared values when using either longer or shorter time steps, and although further research is needed, it's believed the lower r-squared values occur for different reasons. Lower r-squared values for time steps less than 9 minutes likely indicate not enough dispersion via overshoots is occurring, preventing fish from finding optimum habitat. Adjusting the size of the sensory ovoid is one means of compensating for this apparent lack of foresight, but attempts to adjust the 'sensory ovoid' to increase foresight proved ineffective in achieving the appropriate amount of longitudinal dispersion. Lower r-squared values for time steps much greater than 9 minutes likely indicate too much overshooting is occurring in the longitudinal direction. Although distances are large in the longitudinal direction, it seems too much overshooting can take place.

3.4.5.5 *Varying Stimuli/Parameter Weights*

Of all the stimuli parameter weights, three stimuli weights were selected along with the randomization weights for sensitivity analysis. These weights are used, in the NFS, in the comparison of velocity, temperature, and dissolved oxygen gradients to a scaled random number, one of which is chosen by the model to elicit a movement response in the virtual fish. For the analysis, weights

were either increased or decreased from their value in the best parameter set (Appendix C).

Analysis revealed the model is robust enough to handle minor variations in stimuli weights. An increase in the horizontal velocity weight by 20% actually improved upon the 'best' simulation results while a 30% decrease in the temperature weights also failed to significantly deteriorate model results. A 30% decrease in the dissolved oxygen weights seemed to influence model results more so than variations in the other weights. However, it's unsure whether the DO weights actually exceeded some threshold or if the results can be attributed to model variability (3.4.5.6).

The weights for random movement proved to be more important as r-squared values, particularly in the longitudinal direction, suffered significantly when randomization weights decreased. As randomization decreases, other stimuli play a larger role in eliciting movement response. Although not explicit in the sensitivity analysis, perturbations in the randomization weights degrade model results in the longitudinal direction more so than in the vertical direction. This may be attributable to the fact longitudinal movement is more dependent upon randomization and that perturbations likely impair the harmony between randomization and horizontal velocity stimulus responses that dictates much of the longitudinal movement.

3.4.5.6 *Varying the Random Number Generator Seed*

The importance of the random number generator seed lies in its ability to account for, and control for, randomization. The NFS is designed to output the same results over any number of simulations when input parameters, and the random number generator seed, are the same. This allows repeatability of model results. On the other hand, a distribution of results can be obtained for a single parameter set if the random number seed is changed, since portions of the NFS are stochastic. This allows the user to choose between model repeatability and model variability for a given analysis.

To estimate the variability of results when using the best parameter set (Appendix C), the random number seed was varied to obtain a distribution of r-squared values. A total of 31 simulations were run, each differing only in the random number generator seed used. Results of the analysis are shown in Table 3.3 and Figures 3.10 and 3.11.

Table 3.3 Variability of Model Results Using Best Parameter Set.

	R-Squared Value	
Statistic	Longitudinal Distribution	Vertical Distribution
Median	0.61	0.91
Mean	0.60	0.91
Standard Deviation	0.06	0.03
Maximum	0.70	0.95
Minimum	0.49	0.82

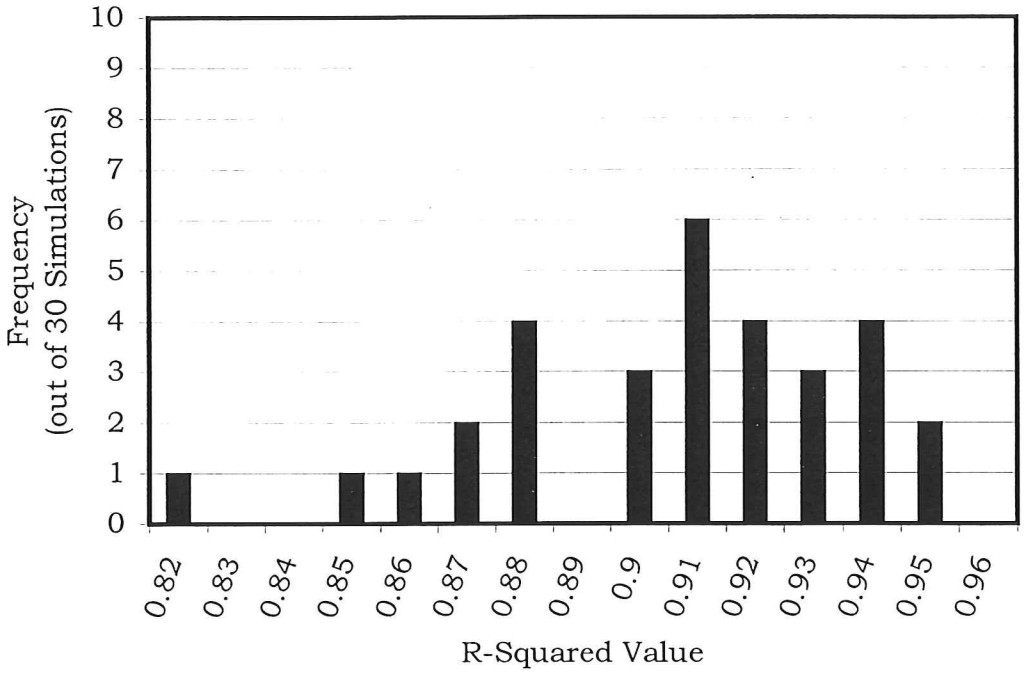


Figure 3.10 Frequency histogram of vertical distribution r-squared values. A total of 31 simulations were run using the best parameter set in which only the random number seed was varied.

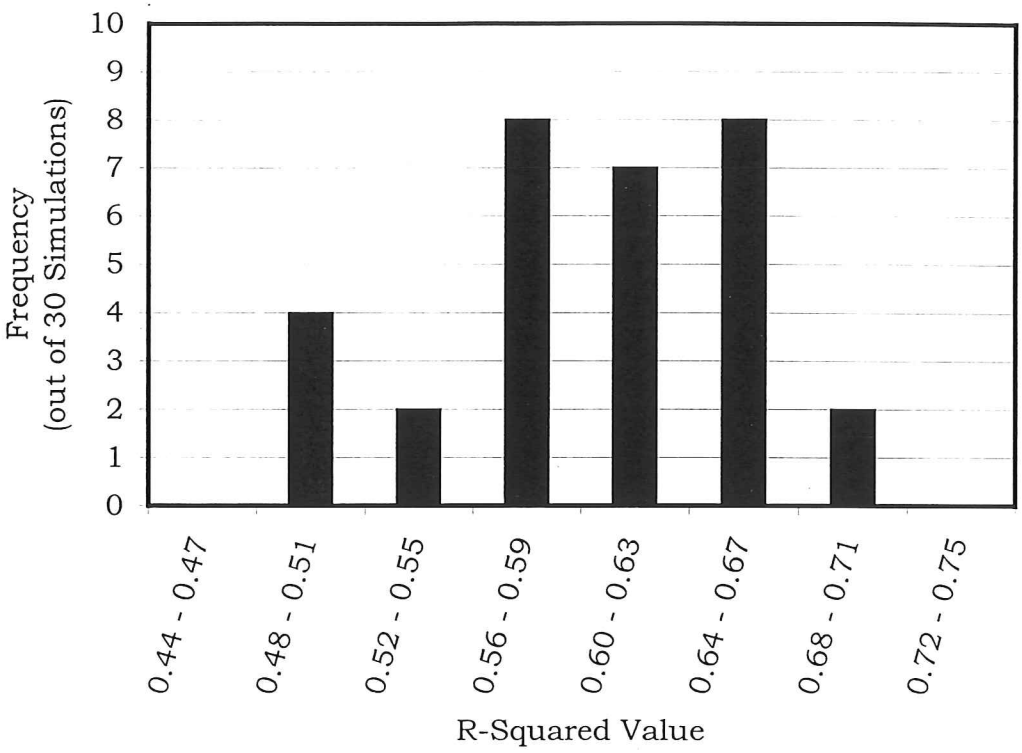


Figure 3.11 Frequency histogram of longitudinal distribution r-squared values. A total of 31 simulations were run using the best parameter set in which only the random number seed was varied.

The figures indicate less variation in vertical distribution r-squared values than in r-squared values for longitudinal distribution. The discrepancy is likely due to the strength of physicochemical gradients in the vertical direction and the heavy reliance of longitudinal movement/dispersion on randomization.

3.5 **Discussion**

Using dynamic flow and water quality simulations as a surrogate for the actual physicochemical regime of JST Lake, the CEL Hybrid Ecological Model performed well in simulating the location and distribution of blueback herring for days in August 1996 when field data existed. Distributions of virtual fish in both the longitudinal and vertical directions indicate substantial similarities to the distributions as detected by actual hydroacoustic surveys. To increase the statistical rigor of the results, the virtual population was sampled in a manner comparable to that used for obtaining the actual field estimates of the blueback herring population distribution.

CEL Hybrid Ecological Models can be used to investigate field observations and hypothesized behaviors for which little or no field data exists. For instance, some literature (e.g., Thomas *et al.*, 1992; Osteen *et al.*, 1989; West *et al.*, 1988; Dadswell, 1985; Meador *et al.*, 1984; Skjeveland, 1982; Loesch and Lund, 1977) suggests that blueback herring are attracted to fast-flowing water, particularly for spawning. High water velocities can be found, among other places, in areas adjacent to intersecting tributaries and where the cross-sectional area changes drastically. The CEL Hybrid Ecological Model developed for this project indicates that blueback herring congregate at six primary locations. Of these locations, four are areas adjacent to intersecting tributaries, one is where lake width

and cross-sectional area changes most drastically, and the last location is the tailrace of RBR Dam.

The tailrace of RBR Dam, in particular, is a place where an increased understanding of blueback herring movement behavior would have immediate ecological, and economic, implications. Blueback herring are observed in the tailrace of RBR Dam in great numbers during pump and/or release operations (Isely, 1996), and blueback herring entraption is a primary concern that impacts the operation of the dam for hydropower generation. The CEL Hybrid Ecological Model provides an opportunity for systematic investigation of the specific flow characteristics that produce unwanted numbers of blueback herring at the dam.

With an increased understanding of the factors influencing blueback herring movement, release strategies, for instance, could be developed that mitigate the flow characteristics, such as flow duration, magnitude, and timing, that attract blueback herring throughout the reservoir to the tailrace. For instance, during warm stratified periods in JST Lake, it may be better to release water from RBR Dam during the day than at night since more tailrace blueback herring could be expected after nighttime releases. This is due to the diel movement of blueback herring and the impact cool water discharge from RBR Dam has on the temperature stratification of JST Lake. Cool water discharge from RBR Dam initially displaces water in the tailrace and replaces it with much cooler water. At some point downstream, however, warmer water creeps to the top of

the displacing cooler water and moves quickly back to the dam displacing cooler water downward. Nighttime releases may result in more blueback herring in the tailrace since blueback herring are nearer the water surface at night and would be more susceptible to transport along with this warm water "kickback". Daytime releases, on the other hand, may catch blueback herring deeper in the water column and move the fish downstream along with the cool water discharge.

3.5.1 **Model Critique**

Given all the assumptions necessary to construct the NFS prototype, I believe the results of the application are very promising. At the same time, however, I acknowledge the apparent complexity of the model and the need for future research and development. Towards this effort, several interesting characteristics of the model's behavior deserve special attention, as I believe these characteristics lend insight into the algorithm enhancements most likely to produce better simulation results. Of model characteristics observed, two deserve attention: the way the model handles longitudinal population dispersion and the interplay between longitudinal and vertical movement.

Currently, the NFS is designed to handle longitudinal population dispersion through the use of random movement. As discussed in Chapter 2, the direction of random movement may change for each fish at every time step depending on the sign of the

random number calculated; both the magnitude and sign of the random number are random. Although only future research into model behavior will tell for certain, I believe this method of achieving longitudinal population dispersion is both insufficient and unrealistic. Under the current mechanics, longer time steps (i.e., much larger than 9 minutes) serve to supplement longitudinal dispersion, which is supposed to be handled exclusively by random movement. At time steps shorter than 9 minutes, fish often congregate near high velocity areas leaving all but a few areas of the virtual reservoir unpopulated. Since distance traveled by the virtual fish is equal to the speed of the fish multiplied by the time step, increasing the time step causes the virtual fish to overshoot optimal habitats at times, resulting in pseudo-dispersion. Modifying the model so random movement is in one direction until a physicochemical stimulus becomes the focus of movement (although swimming velocity may change) is likely to produce the longitudinal population dispersion needed, without the need to manipulate the time step. Most importantly, however, support for enhancing the model's handling of horizontal random movement comes from the field. Field research indicates that the movement of organisms lies somewhere between random walk and straight movement paths (Tischendorf, 1997). For blueback herring, a pelagic species, this is probably particularly true. In addition, Janssen (1982) compared the search behavior of bluegills (*Lepomis machrochirus*) and blueback herring and found that blueback herring swim as they

search while bluegills searched from a stationary location. The random movement (or search behavior) of blueback herring is, thus, probably an important dynamic to capture realistically.

The interplay between horizontal and vertical movement is complex, probably due to the long time steps required for supplementing longitudinal dispersion under the current algorithm. The long time steps needed work in opposition to the shorter time steps that produce excellent distributions in the vertical direction. Although not explicit in the sensitivity analysis, shorter time steps were often associated with exceptional vertical distributions of the virtual population, sometimes garnering r-squared values as high as 0.98 when compared to the actual vertical distribution. Attempts to mitigate the negative impact longer time steps have on the vertical distribution through the use of slower vertical swim speeds proved ineffective. Likewise, increasing the longitudinal axis of the sensory ovoid (Chapter 2) to increase/maintain longitudinal foresight while setting the time step near the optimum of 5 minutes for vertical movement also proved ineffective at reconciling the negative interplay between longitudinal and vertical movement. Investigating the nonharmonious relationship between longitudinal and vertical movement and the time step would prove beneficial. On the other hand, this problem may fade with the advent of a solution to achieving better longitudinal population dispersion using random movement.

3.6 **Conclusion**

The CEL Hybrid Ecological Modeling System provides a systematic framework for integrating biological knowledge and field experience into engineering physicochemical simulation models. In the model, a Numerical Fish Surrogate was used to translate existing field knowledge into an algorithm capable of being integrated into a hydrodynamic and water quality model. The CEL Hybrid Ecological Model that resulted reproduced the distribution of blueback herring in J. Strom Thurmond Lake for dates when field data existed.

While realism of the predictions was of primary focus in developing the model, I believe that concentrating on the inevitable shortcomings short circuit the overall effort. To this end, I believe that additional research and further application of the model will result in relatively quick resolution of many of the shortcomings. My goal was to develop a framework that possesses real opportunities for simulating population processes in a realistic context and a framework that can be readily enhanced with further research. Representing an infinitely complex dynamic behavioral system using finite means will always result in shortcomings and inaccuracies. However, I believe the results obtained from this CEL Hybrid Ecological Model application provide promise that systematic and realistic simulation of many population processes, particularly movement behavior, is possible.

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APPENDIX A

Input Variables for Numerical Fish Surrogate

A.1 **Parameters Needing Calibration**

NFSFREQ = The number (or fraction thereof) of days between successive runs of the Numerical Fish Surrogate (NFS) module.

A.1.1 Sensory Weight and Scaling Parameters

MULTIPLERESPONSE = If TRUE, the URGENCY variable is calculated as a weighted average of the selected scaled horizontal velocity, vertical velocity, dissolved oxygen, and temperature gradients. If FALSE, the URGENCY variable is calculated as the maximum of the following: horizontal velocity, vertical velocity, dissolved oxygen, and temperature gradients.

A.1.1.1 Horizontal Gradient Parameters: (Range: 0 to 1)

HVXWEIGT = Weight for x-directional horizontal velocity gradient.

VVXWEIGT = Weight for x-directional vertical velocity

gradient.

TPXWEIGT = Weight for x-directional temperature gradient.

DOXWEIGT = Weight for x-directional dissolved oxygen gradient.

A.1.1.2 Vertical Gradient Parameters: (Range: 0 to 1)

HVZWEIGT = Weight for z-directional horizontal velocity gradient.

VVZWEIGT = Weight for z-directional vertical velocity gradient.

TPZWEIGT = Weight for z-directional temperature gradient.

DOZWEIGT = Weight for z-directional dissolved oxygen gradient.

A.1.1.3 Stepwise Linear Gradient Function Parameters:

TEMPTHRES = Temperature threshold (°C), above which fish will swim with maximum URGENCY toward cooler water.

TSTEP1 = Temperature difference (°C) above and below the optimum, beyond which URGENCY is multiplied by TSTEP1MULT.

TSTEP1MULT = Increase/decrease multiplier in URGENCY when fish is located beyond TSTEP1 from

optimum temperature.

TSTEP2 = Temperature difference (°C) above and below the optimum, beyond which URGENCY is multiplied by TSTEP2MULT.

TSTEP2MULT = Increase/decrease multiplier in URGENCY when fish is located beyond TSTEP2 from optimum temperature.

DOTHRES2 = Dissolved oxygen threshold (mg/L), above which fish will swim with less URGENCY.

DOSTEP1MULT = Increase/decrease multiplier in URGENCY when fish is located in dissolved oxygen concentrations greater than DOTHRES2.

A.1.1.4 Primary Random Displacement Parameters: (Range: 0 to 1)

RDXWEIGT = Weight for x-directional random movement.

RDYWEIGT = Weight for y-directional random movement.

RDZWEIGT = Weight for z-directional random movement.

A.1.1.5 Other Random Displacement Parameters:

EPSILONRD = Random Parameter Epsilon - Used only to keep RDX, RDY, and RDZ from getting stuck on zero when UFISH, VFISH, or WFISH = 0, respectively.

A.1.1.6 The following values are used to scale the gradients each fish detects within its sensory sphere. The parameters immediately below should be valued according to the gradient likely to induce the maximum fish response; with higher magnitude gradients not inducing any more of a response from the species of fish under study. The following parameters define a representative example of the practical maximum gradient likely to induce the greatest fish response/reaction/movement. ALL NUMBERS MUST BE POSITIVE.

Horizontal Velocity

X-directional Gradient

MAXREACTXHV = For example gradient, the higher horizontal velocity value (m/s) in x-direction.

MINREACTXHV = For example gradient, the lower horizontal velocity value (m/s) in x-direction.

DISTREACTXHV = For example gradient, the distance between MAXREACTXHV and MINREACTXHV (m).

Z-directional Gradient

MAXREACTZHV = For example gradient, the higher horizontal velocity value (m/s) in z-direction.

MINREACTZHV = For example gradient, the lower horizontal velocity value (m/s) in

z-direction.

DISTREACTZHV = For example gradient, the distance between MAXREACTZHV and MINREACTZHV (m).

Vertical Velocity

X-directional Gradient

MAXREACTXVV = For example gradient, the higher vertical velocity value (m/s) in x-direction.

MINREACTXVV = For example gradient, the lower vertical velocity value (m/s) in x-direction.

DISTREACTXVV = For example gradient, the distance between MAXREACTXVV and MINREACTXVV (m).

Z-directional Gradient

MAXREACTZVV = For example gradient, the higher vertical velocity value (m/s) in z-direction.

MINREACTZVV = For example gradient, the lower vertical velocity value (m/s) in z-direction.

DISTREACTZVV = For example gradient, the distance between MAXREACTZVV and

MINREACTZVV (m).

Temperature

X-directional Gradient

MAXREACTXTP = For example gradient, the higher temperature value (°C) in x-direction.

MINREACTXTP = For example gradient, the lower temperature value (°C) in x-direction.

DISTREACTXTP = For example gradient, the distance between MAXREACTXTP and MINREACTXTP (m).

Z-directional Gradient

MAXREACTZTP = For example gradient, the higher temperature value (°C) in z-direction.

MINREACTZTP = For example gradient, the lower temperature value (°C) in z-direction.

DISTREACTZTP = For example gradient, the distance between MAXREACTZTP and MINREACTZTP (m).

Dissolved Oxygen

X-directional Gradient

MAXREACTXDO = For example gradient, the higher

dissolved oxygen value (mg/L) in x-direction.

MINREACTXDO = For example gradient, the lower dissolved oxygen value (mg/L) in x-direction.

DISTREACTXDO = For example gradient, the distance between MAXREACTXDO and MINREACTXDO (m).

Z-directional Gradient

MAXREACTZDO = For example gradient, the higher dissolved oxygen value (mg/L) in z-direction.

MINREACTZDO = For example gradient, the lower dissolved oxygen value (mg/L) in z-direction.

DISTREACTZDO = For example gradient, the distance between MAXREACTZDO and MINREACTZDO (m).

A.1.2 Sensory Sphere Parameters

FBDYSEARCH = The number of body lengths (FSIZE) in front of the fish the fish will likely search during each time step to determine conditions/gradients.

BBDYSEARCH = The number of body lengths (FSIZE) behind

the fish the fish will likely search during each time step to determine conditions/gradients.

UBDYSEARCH = The number of body lengths (FSIZE) above the fish the fish will likely search during each time step to determine conditions/gradients.

DBDYSEARCH = The number of body lengths (FSIZE) below the fish the fish will likely search during each time step to determine conditions/gradients.

A.1.3 Miscellaneous Parameters

TEMPOPTD = Optimum temperature for fish species during the day (°C).

TEMPOPTN = Optimum temperature for fish species at night (°C).

MXXSPDL = Number of fish lengths (FSIZE) covered in x-direction per second at maximum fish speed under perfect conditions.

MXZSPDL = Number of fish lengths (FSIZE) covered in z-direction per second at maximum fish speed under perfect conditions.

DOTHRES = Dissolved oxygen threshold below which fish

swimming speed suffers.

XREFL = Fish reflected this percentage of segment length when fish encounters horizontal boundary.

YREFL = Fish reflected this percentage of cell width when fish encounters lateral boundary.

ZBOTREFL = Fish reflected this percentage of bottom layer height when fish encounters bottom.

ZSURREFL = Fish reflected this percentage of surface layer height when fish encounters water surface.

A.2 **Parameters Not Needing Calibration**

A.2.1 Virtual Sampling Parameters

A.2.1.1 Virtual Gillnets

GILLNETSAMPLING = If TRUE, virtual gillnet sampling is permitted.

DEPTHINT = Depth interval (m) used to display gillnet results; (positive number).

GILLNETS(#,1) = Day (INTEGER) to start gillnet sampling.

GILLNETS(#,2) = Day (INTEGER) to end gillnet sampling.

GILLNETS(#,3) = Hour (Military Time) to start gillnet sampling.

GILLNETS(#,4) = Hour (Military Time) to end gillnet sampling.

GILLNETS(#,5) = X-location (m) downstream from upstream end of water body where gillnet is placed.

GILLNETS(#,6) = Width (meters from center of water body) that the gillnet extends towards left bank; (negative number).

GILLNETS(#,7) = Width (meters from center of water body) that the gillnet extends towards right bank; (positive number).

GILLNETS(#,8) = Depth below water surface (m) to top of gillnet; (positive number).

GILLNETS(#,9) = Depth below water surface (m) to bottom of gillnet; (positive number).

GILLNETS(#,10) = Gillnet #.

GILLNETS(#,11) = Gillnet active: [0 = No , 1 = Yes].

GILLNETS(#,12) = Water body branch number where gillnet is placed.

A.2.1.2 Virtual Hydroacoustics

ACOUSTICSAMPLING = If TRUE, virtual hydroacoustic sampling is permitted.

HADEPTHINT = Depth interval (m) used to display hydroacoustic sampling results; (positive number).

HAOPERAT(#,1) = Day (INTEGER) to start hydroacoustic

survey.

HAOPERAT(#,2) = Day (INTEGER) to end hydroacoustic survey.

HAOPERAT(#,3) = Hour (Military Time) to start hydroacoustic survey.

HAOPERAT(#,4) = Hour (Military Time) to end hydroacoustic survey.

HAOPERAT(#,5) = X-location (m) of upstream end of hydroacoustic sampling 'box' at start of survey.

HAOPERAT(#,6) = X-location (m) of downstream end of hydroacoustic sampling 'box' at start of survey.

HAOPERAT(#,7) = Speed (m/s) of hydroacoustic sampling 'box':

(-) = moves upstream

(+) = moves downstream

HAOPERAT(#,8) = Width (meters from center of water body) that the hydroacoustic sampling 'box' extends towards the left bank; (negative number).

HAOPERAT(#,9) = Width (meters from center of water body) that the hydroacoustic sampling 'box' extends towards the right bank;

(positive number).

HAOPERAT(#,10) = Depth below water surface (m) to top of hydroacoustic sampling 'box';
(positive number)

HAOPERAT(#,11) = Depth below water surface (m) to bottom of hydroacoustic sampling 'box';
(positive number).
May overestimate depth in order to cover the entire water column, if so desired.

HAOPERAT(#,12) = Hydroacoustic sampling operation #.

HAOPERAT(#,13) = Hydroacoustic sampling active:
[0 = No , 1 = Yes].

HAOPERAT(#,14) = Water body branch number where hydroacoustic survey is conducted.

A.2.2 Output frequency from Numerical Fish Surrogate for graphics post processing. May enter '99' in order to skip output for a particular month altogether:

OUTFREQJAN = for January

OUTFREQFEB = for February

OUTFREQMAR = for March

OUTFREQAPR = for April

OUTFREQMAY = for May

OUTFREQJUN = for June

OUTFREQJUL = for July

OUTFREQAUG = for August

OUTFREQSEP = for September

OUTFREQOCT = for October

OUTFREQNOV = for November

OUTFREQDEC = for December

A.2.3 Activation of Stimuli-Response Rules

STIMULIRULES = If TRUE, stimuli-response rules (excluding passive transport which is specified separately) contribute to fish movement.
If FALSE, stimuli-response rules (excluding passive transport which is specified separately) do not contribute to fish movement.

VELOCITYRULES = If TRUE, velocity stimuli-response rules contribute to the movement of fish.
If FALSE, velocity stimuli-response rules do not contribute to the movement of fish.

TEMPRULES = If TRUE, temperature stimuli-response rules contribute to the movement of fish.
If FALSE, temperature stimuli-response rules do not contribute to the movement

of fish.

DORULES = If TRUE, dissolved oxygen stimuli-response rules contribute to the movement of fish.
If FALSE, dissolved oxygen stimuli-response rules do not contribute to the movement of fish.

RANDOMIZATION = If TRUE, random displacement terms (i.e., RDX, RDY, RDZ) are calculated.
If FALSE, random displacement terms (i.e., RDX, RDY, RDZ) are set to zero.

PASSIVETRANSPORT = If TRUE, passive transport contributes to the displacement of fish.
If FALSE, passive transport does not contribute to the displacement of fish.

A.2.4 Miscellaneous Parameters

DEBUG = If TRUE, user informed when important steps are completed successfully.
If FALSE, no extra output generated that may assist in debugging the Numerical Fish Surrogate.

WBSKIP = If TRUE, output files will be generated for water body WBRUN only.
If FALSE, output files will be generated for all

water bodies. This requires much more computer disk space.

WBRUN = If WBSKIP = TRUE, output files will be generated for this water body only.

LINEAR = If TRUE, velocity interpolation scheme is linear interpolation.
If FALSE, velocity interpolation scheme is 3rd Order Newton interpolation.

PREVENTBRCHSWITCH = If TRUE, fish are prevented from swimming upstream into another branch.
If FALSE, fish may swim upstream into other branches.

UNBP = The branch at who's upstream end fish are collected.

DNBP = The branch at who's downstream end fish are collected. This must be the branch which has no branch downstream of it.

SEED = Seed for the random number generator.

A.2.5 Graphics Post Processing Parameters

ASPRATIO = Scaling coefficient for vertical velocity vectors; velocities only scaled for graphical display.

SHOWSKY = If TRUE, cells above the water surface will be colored according to the time of day.
If FALSE, cells above the water surface will be

blank (i.e., colored white).

SKYNIGHT = The time of day when night begins; after which sky is black (military time).

SKYDAWN = The time of day when morning begins; after which sky is yellow (military time).

SKYDAY = The time of day when 'day' begins; after which sky is blue (military time).

SKYDUSK = The time of day when evening begins; after which sky is orange (military time).

A.2.6 Fish Parameters

DELAYDATE = Date (JDAY) to begin modeling fish movement (i.e., date to 'release' fish).

FISHES(#,1) = Initial segment IMP where fish is placed.

FISHES(#,2) = Location of fish within segment IMP from upstream end (m).

FISHES(#,3) = Initial layer KMP where fish is placed.

FISHES(#,4) = Location of fish within layer KMP from top (m).

FISHES(#,5) = Lateral location in channel of fish placement (m) (from left bank in plan view).

FISHES(#,6) = Branch where fish is placed.

FISHES(#,7) = Size (i.e., length) of fish (m) (1 inch = 0.0254 meters).

FISHES(#,8) = Age of fish (info not currently used in

NFS).

FISHES(#,9) = Initial longitudinal swimming velocity (m/s) of the fish relative to water:
(-) = swimming upstream
(+) = swimming downstream

FISHES(#,10) = Initial lateral swimming velocity (m/s) of the fish relative to water:
(-) = swimming towards left bank
(+) = swimming towards right bank

FISHES(#,11) = Initial vertical swimming velocity (m/s) of the fish relative to water:
(-) = swimming towards the water surface
(+) = swimming towards the water bottom

FISHES(#,12) = Is fish still in system: [0 = Yes , 1 = No]

FISHES(#,13) = Gillnet # fish is snagged in; = 0 if fish not in a gillnet.

APPENDIX B

FORTRAN Subroutines Comprising the Numerical Fish Surrogate

SUBROUTINE FISH

This is the only subroutine called from the CE-QUAL-W2 main program. All other subroutines that comprise the Numerical Fish Surrogate are called from this subroutine. This subroutine contains the equations discussed in Chapter 2 and checks to make sure all fish stay within the boundaries of the system.

SUBROUTINE RANDOM

This subroutine calculates a random number between 0 and 1, which is later used in determining random movement.

SUBROUTINE FIMPBR

This subroutine is run only once and determines the longitudinal segments within the system grid that have incoming branches (i.e., tributaries). This alerts the main subroutine (FISH) to pay careful attention to virtual fish within these segments, as pseudo lateral forcing functions are created to allow fish to move upstream and downstream into adjoining branches.

SUBROUTINE FINDNEWBR

This subroutine determines what branch the virtual fish is located in.

SUBROUTINE WHATJR

This subroutine determines what water body the virtual fish is located in.

SUBROUTINE TAG124578

This subroutine calculates pseudo lateral forcing functions (i.e., lateral flow values) in segments where there is one incoming branch and determines if the virtual fish is swept upstream or downstream into the adjoining branch.

SUBROUTINE TAG369

This subroutine calculates pseudo lateral forcing functions (i.e., lateral flow values) in segments where there are two incoming branches and determines if the virtual fish is swept upstream or downstream into either of the adjoining branches.

SUBROUTINE GRIDPLOT

This subroutine converts the structured grid of CE-QUAL-W2 into a finite-difference grid, which is then used by the Numerical Fish Surrogate. The subroutine also outputs flow and water quality information over time to files used in graphics post processing.

SUBROUTINE INTERCONST

This subroutine 'moves' water quality information from the cell centers to the cell nodes by interpolating the constituent values using a bilinear spline method.

SUBROUTINE INTERFLOWF

This subroutine 'moves' hydraulic information from the cell faces to the cell nodes by interpolating the flow values using a 3rd Order Newton interpolation polynomial.

SUBROUTINE FISHPLOT

This subroutine outputs fish positions over time to files used in graphics post processing.

SUBROUTINE SPLINE

This subroutine calculates the flow and water quality values at each of the four cardinal locations of the fish sensory sphere using a bilinear spline interpolation method.

SUBROUTINE VGILLNETS

This subroutine samples the simulated system with virtual gillnets. Fish caught in virtual gillnets are summarized in the end as the number of fish caught per depth interval. Fish caught in the virtual gillnets are stuck and cannot move until the virtual gillnet is removed.

SUBROUTINE ACOUSTICS

This subroutine samples the simulated system with hydroacoustics. Fish that cross the hydroacoustic beam (simulated as a 3-D column) are tallied and summarized in the end as the number of fish detected per depth interval.

APPENDIX C

Parameter Set for Best Simulation Run

Numerical Fish Surrogate Diagnostic Output

Null Water Quality Field:	OFF
Null Hydrodynamic Field:	OFF
Passive Transport:	ON
Schooling Behavior:	OFF
Multi-Response Behavior:	OFF
Stimuli-Response Rules:	ON
- Velocity Rules:	ON
- Temperature Rules:	ON
- Diss Oxygen Rules:	ON
- Randomization:	ON

Numerical Fish Surrogate Timestep (JDAY)

NFSFREQ = 0.00625 (9 minutes)

Weights of Influence Parameters (Range: 0 --> 1)

Horizontal Velocity Parameters

HVXWEIGT = 1.0

VVXWEIGT = 0.3

Vertical Velocity Parameters

HVZWEIGT = 0.2

VVZWEIGT = 0.1

Temperature Parameters

TPXWEIGT = 0.90

TPZWEIGT = 0.75

TEMPTHRES = 26.0

TSTEP1 = 1.5

TSTEP1MULT = 0.0

TSTEP2 = 3.5

TSTEP2MULT = 0.5

Dissolved Oxygen Parameters

DOXWEIGT = 0.76

DOZWEIGT = 0.12

DOTHRES2 = 6.5

DOSTEP1MULT = 0.10

Random Displacement Parameters

RDXWEIGT = 0.999

RDYWEIGT = 0.5

RDZWEIGT = 0.47

EPSILONRD= 1.0E-09

Values Used to Scale the Influence Parameters Gradients

Horizontal Velocity

X-direction

MAXREACTXHV = 0.035

MINREACTXHV = 0.0

DISTREACTXHV = 1

Z-direction

MAXREACTZHV = 0.01

MINREACTZHV = 0.001

DISTREACTZHV = 0.135

Vertical Velocity

X-direction

MAXREACTXVV = 0.01

MINREACTXVV = 0.001

DISTREACTXVV = 3000

Z-direction

MAXREACTZVV = 0.01

MINREACTZVV = 0.001

DISTREACTZVV = 110

Temperature

X-direction

MAXREACTXTP = 30

MINREACTXTP = 15

DISTREACTXTP = 1700

Z-direction

MAXREACTZTP = 30

MINREACTZTP = 15

DISTREACTZTP = 3.80

Dissolved Oxygen

X-direction

MAXREACTXDO = 8

MINREACTXDO = 4

DISTREACTXDO = 7000

Z-direction

MAXREACTZDO = 8

MINREACTZDO = 4

DISTREACTZDO = 3.80

SENSORY SPHERE Parameters

FBDYSEARCH = 7500

BBDYSEARCH = 7500

UBDYSEARCH = 100

DBDYSEARCH = 100

MISC Parameters

TEMPOPTD = 17.0

TEMPOPTN = 22.5

MXXSPDL = 12.0

MXZSPDL = 0.13

DOTHRES = 6.0

XREFL = 0.1

YREFL = 0.1

ZBOTREFL = 2.0

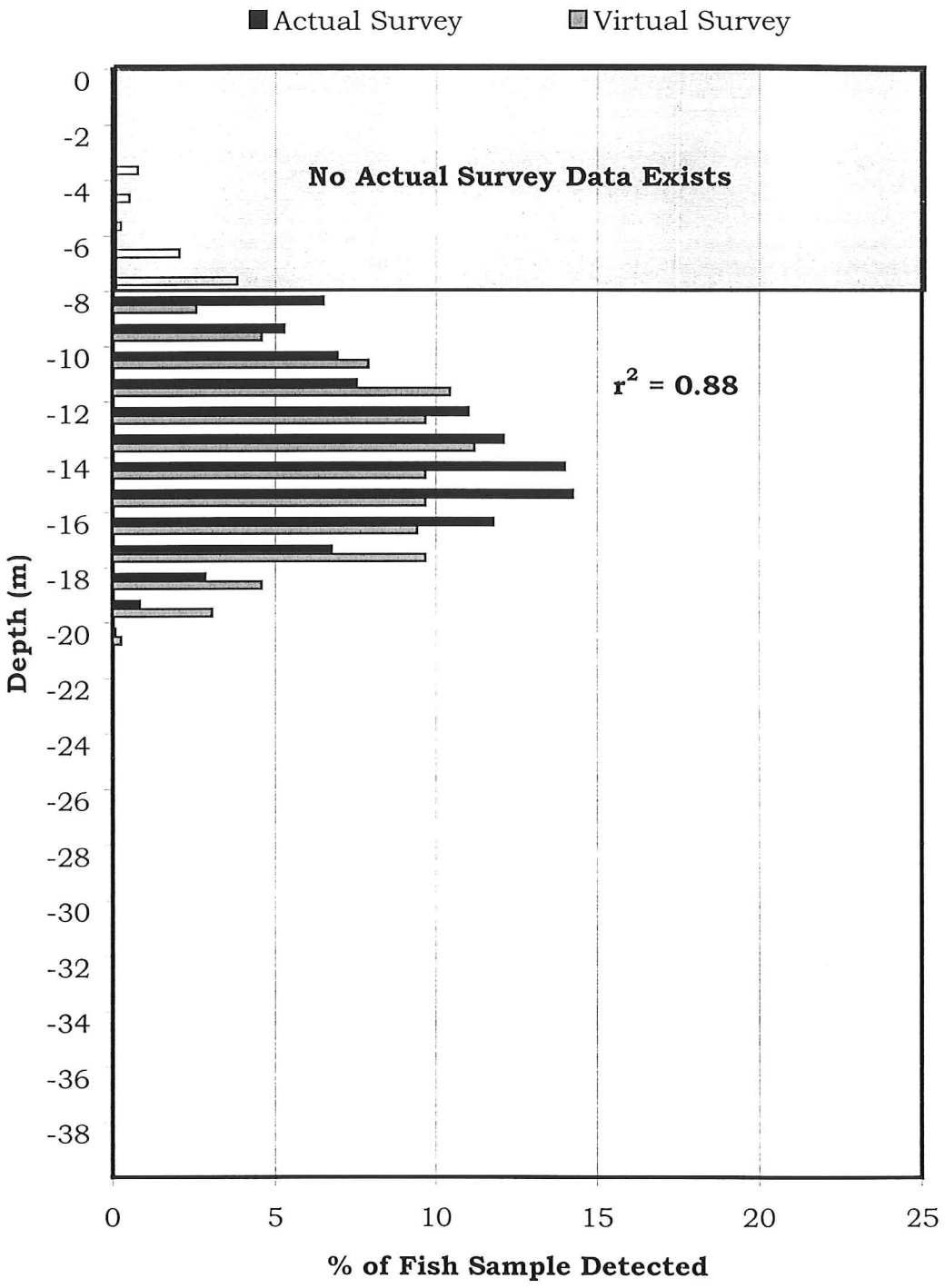
ZSURREFL = 0.5

FSIZE = 0.178

APPENDIX D

Graphs of Sensitivity Analysis Simulation Results

Figure D.1 Vertical distribution of blueback herring as given by both actual and virtual hydroacoustic surveys. This simulation used 5600 virtual fish instead of the 8960 used for the best simulation.


Actual Survey
Virtual Survey
No Actual Survey Data Exists
r^2 = 0.88
Depth (m)
0
-2
-4
-6
-8
-10
-12
-14
-16
-18
-20
-22
-24
-26
-28
-30
-32
-34
-36
-38
0
5
10
15
20
25
% of Fish Sample Detected

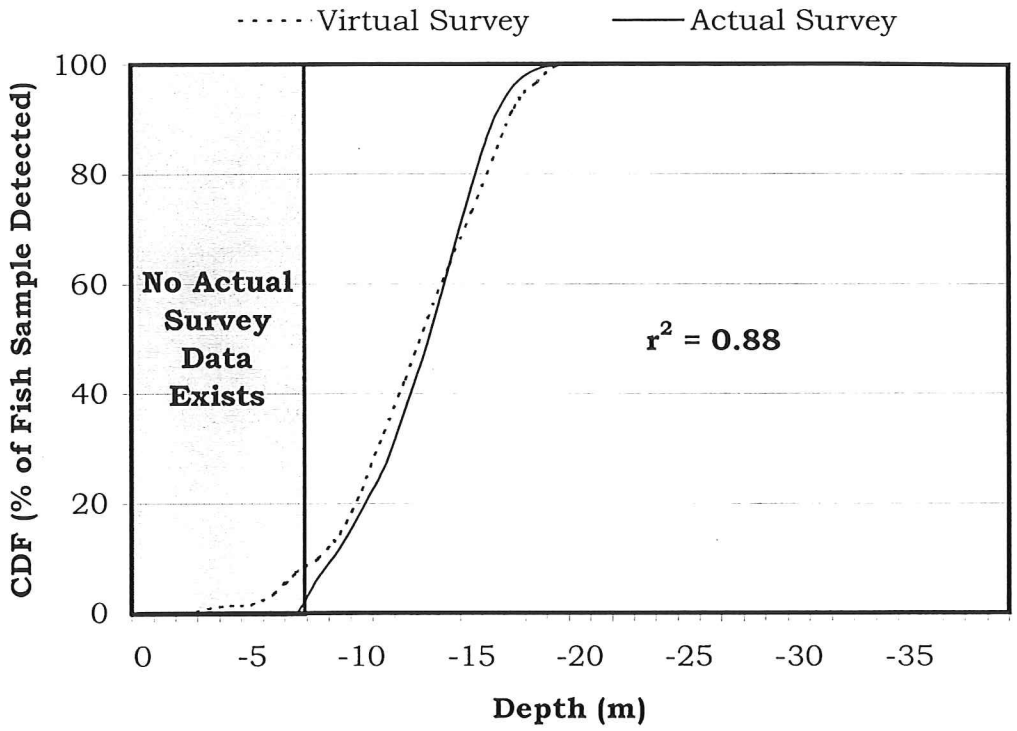


Figure D.2 Cumulative Distribution Function (CDF) showing the amount of the survey sample detected by depth. This simulation used 5600 virtual fish instead of the 8960 used for the best simulation.

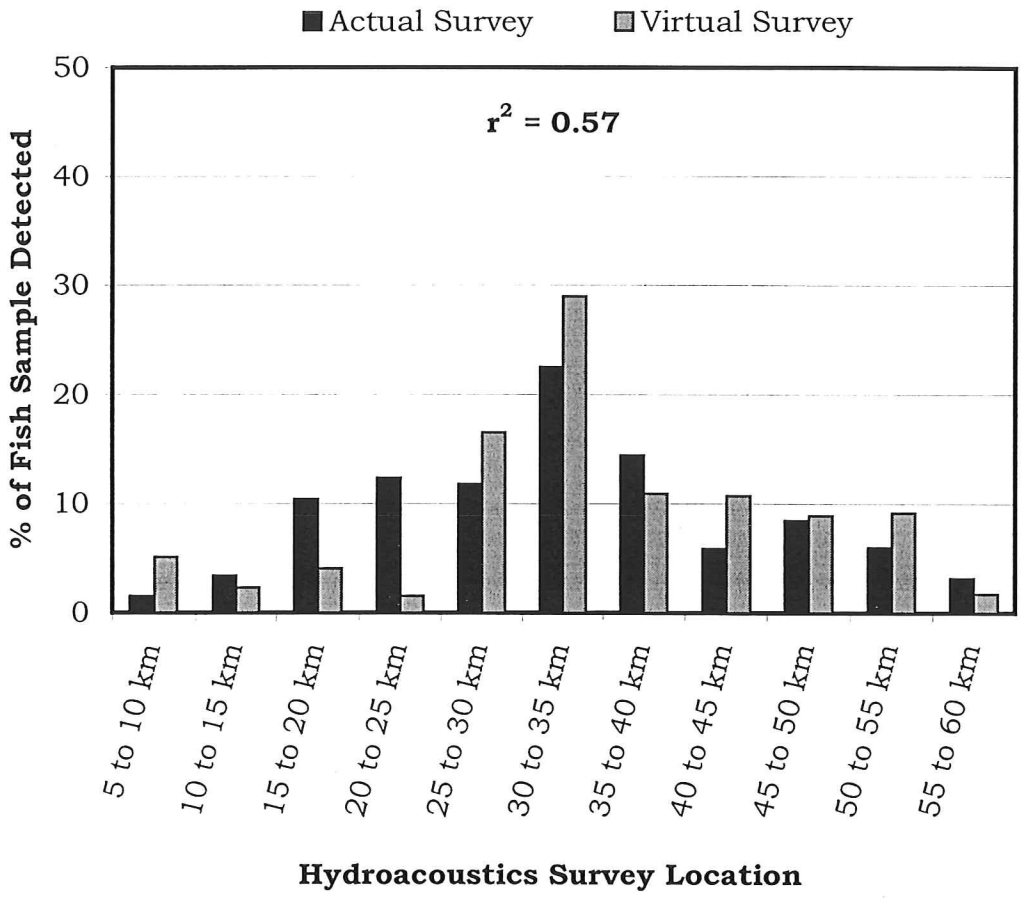


Figure D.3 Longitudinal distribution of blueback herring as given by both actual and virtual hydroacoustic surveys. This simulation used 5600 virtual fish instead of the 8960 used for the best simulation.

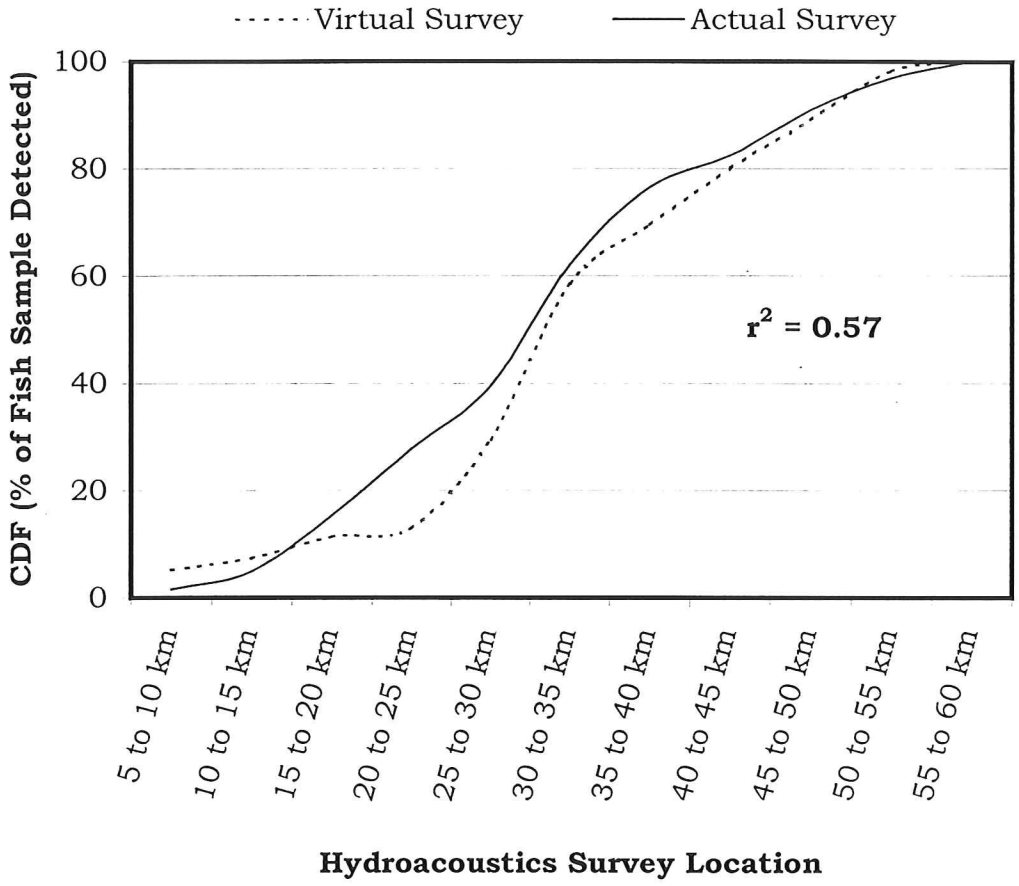
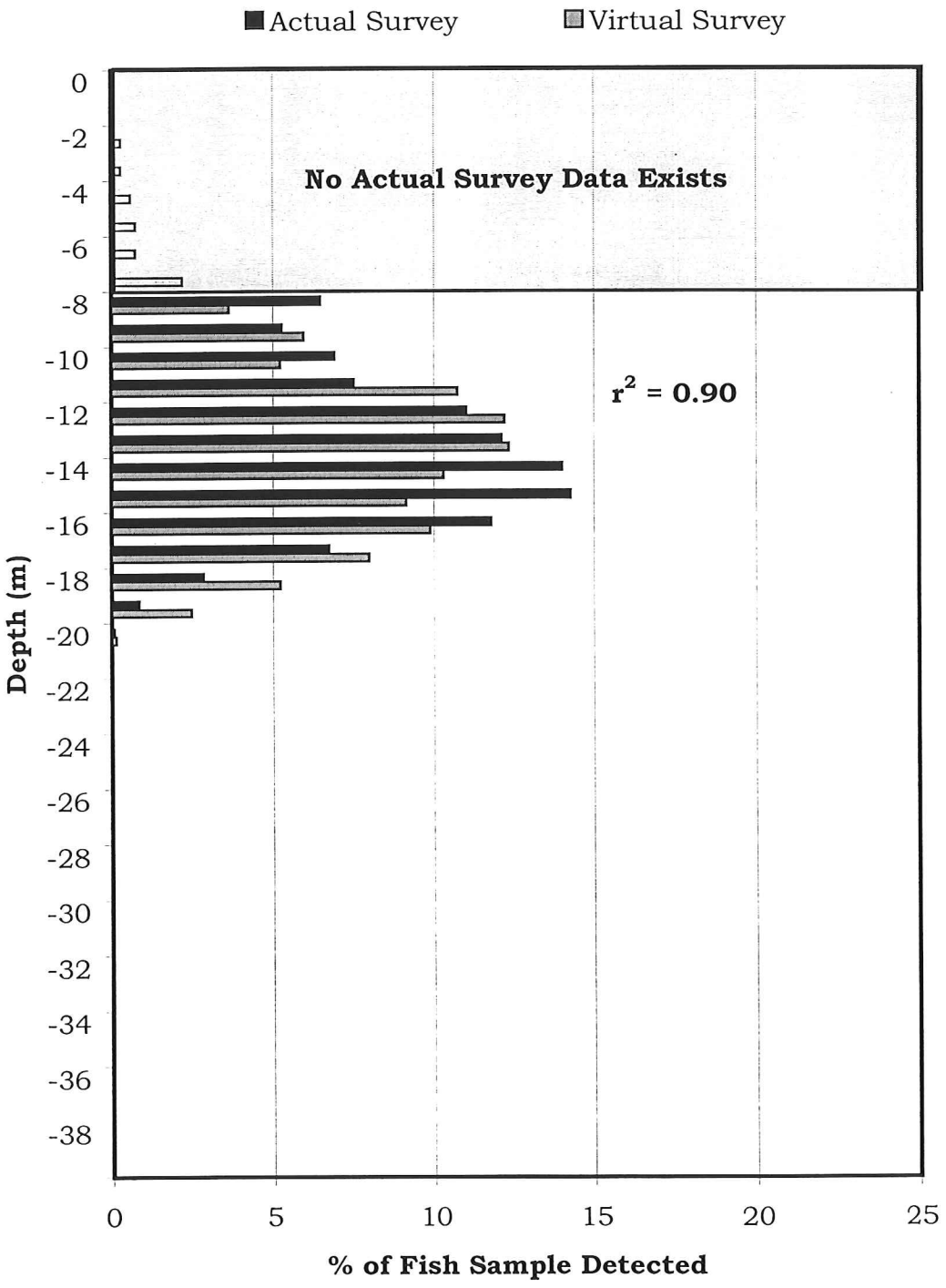


Figure D.4 Cumulative Distribution Function (CDF) showing the amount of the survey sample detected by distance downstream from RBR Dam. This simulation used 5600 virtual fish instead of the 8960 used for the best simulation.

Figure D.5 Vertical distribution of blueback herring as given by both actual and virtual hydroacoustic surveys. This simulation used 11,200 virtual fish instead of the 8960 used for the best simulation.


Actual Survey
Virtual Survey
No Actual Survey Data Exists
r^2 = 0.90
Depth (m)
0
-2
-4
-6
-8
-10
-12
-14
-16
-18
-20
-22
-24
-26
-28
-30
-32
-34
-36
-38
0
5
10
15
20
25
% of Fish Sample Detected

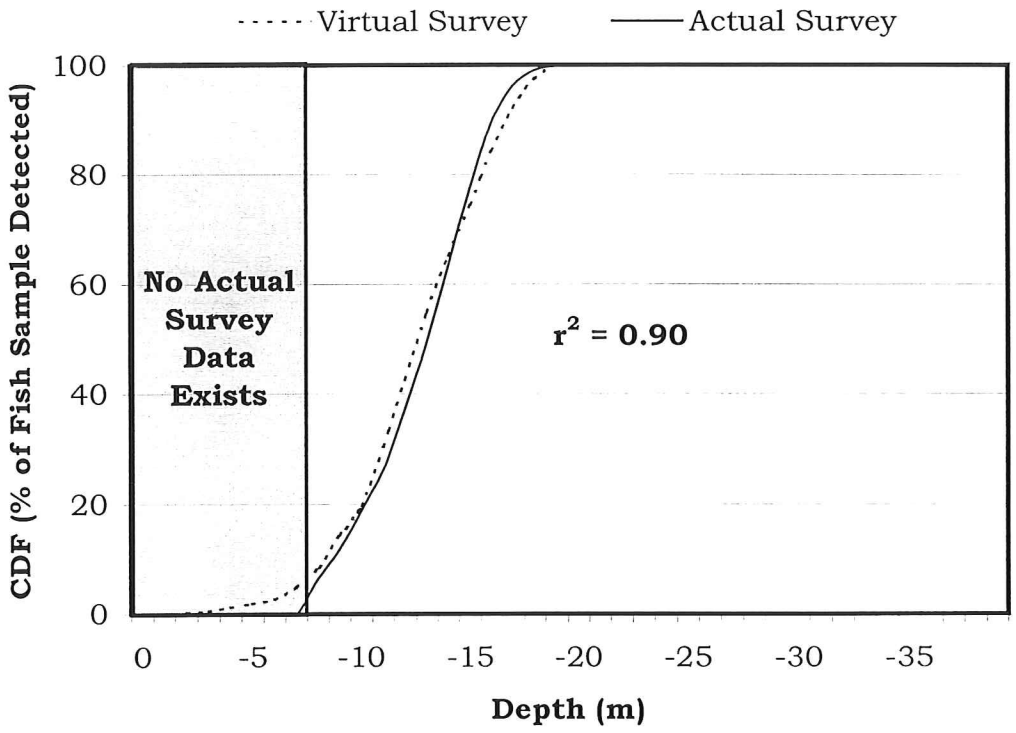


Figure D.6 Cumulative Distribution Function (CDF) showing the amount of the survey sample detected by depth. This simulation used 11,200 virtual fish instead of the 8960 used for the best simulation.

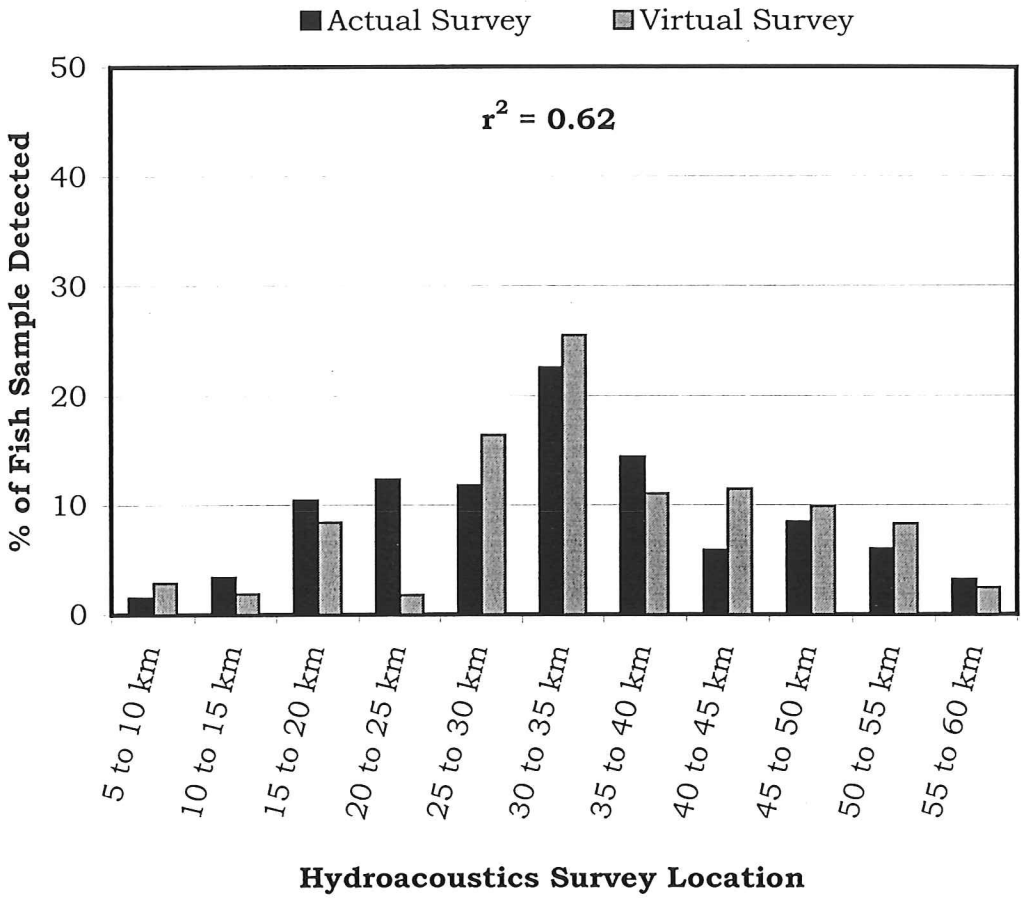


Figure D.7 Longitudinal distribution of blueback herring as given by both actual and virtual hydroacoustic surveys. This simulation used 11,200 virtual fish instead of the 8960 used for the best simulation.

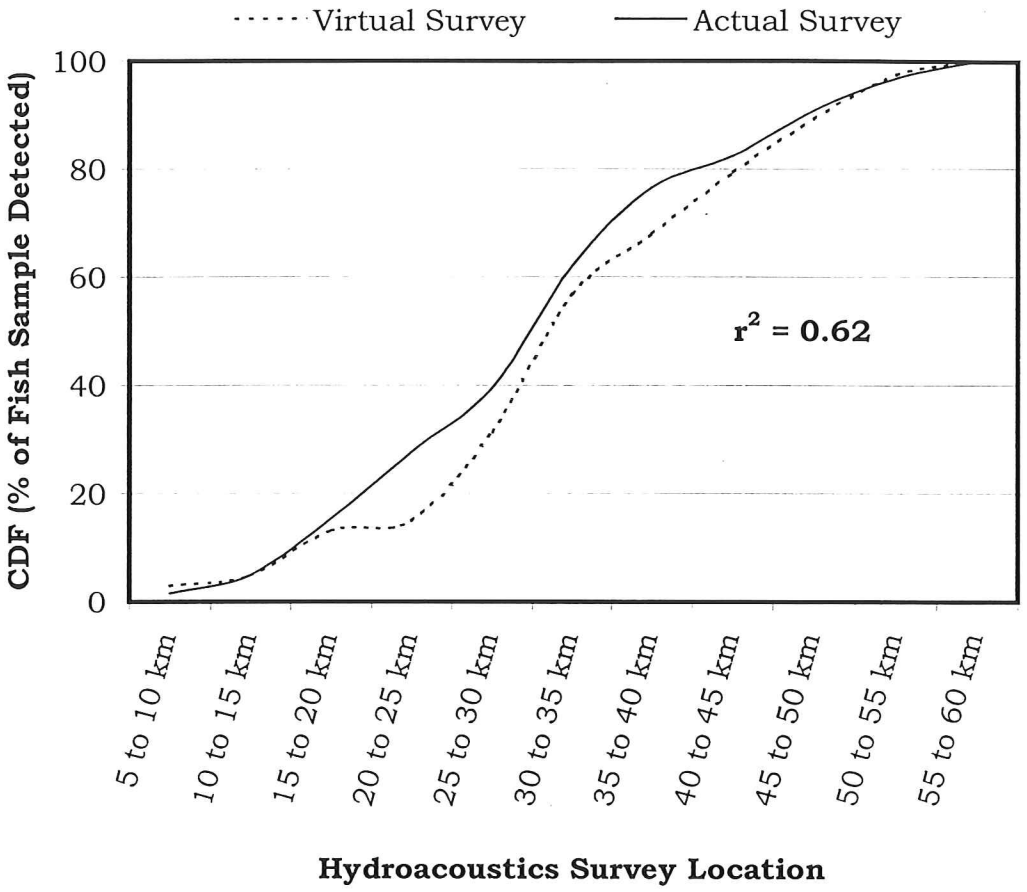
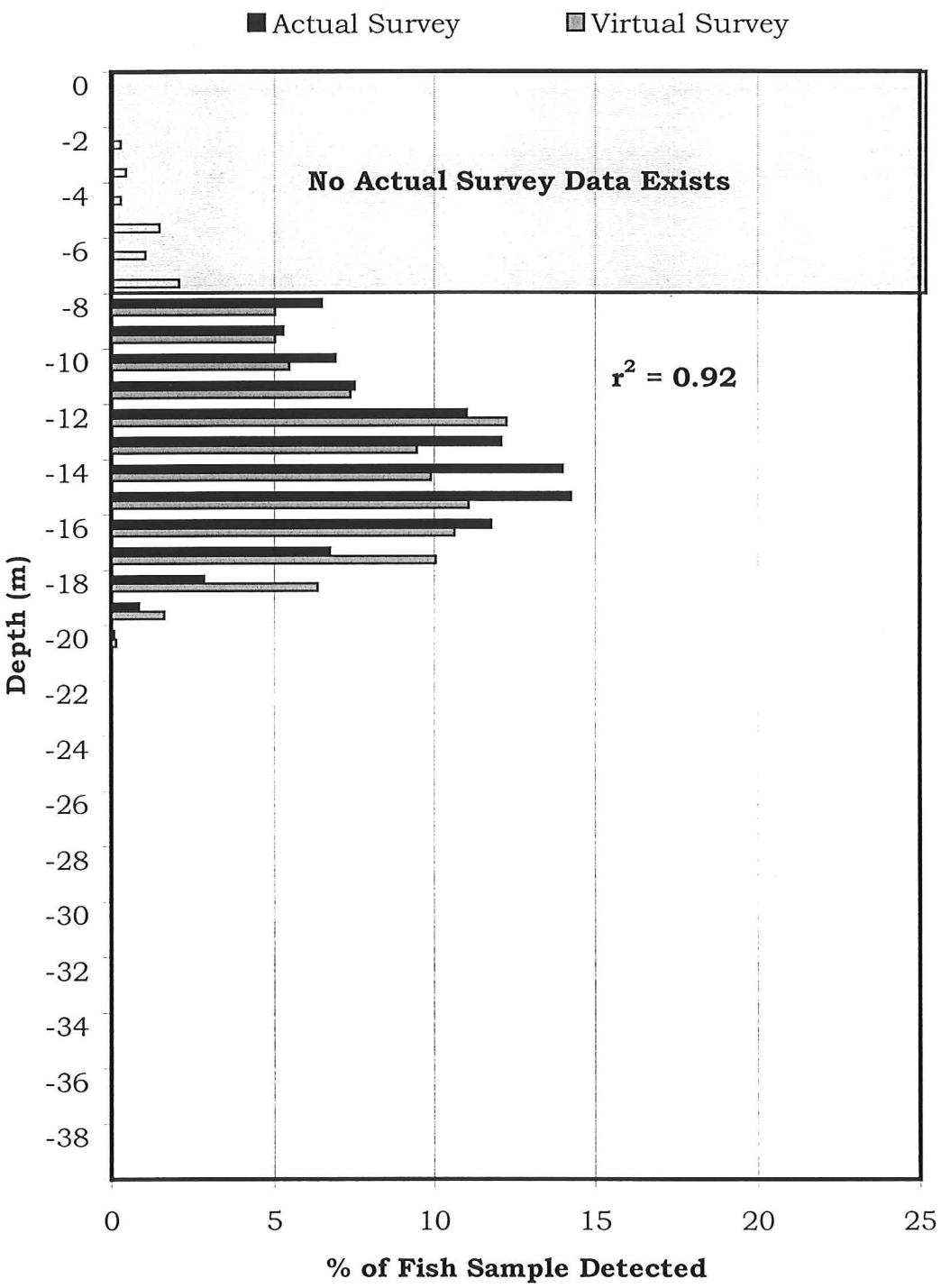


Figure D.8 Cumulative Distribution Function (CDF) showing the amount of the survey sample detected by distance downstream from RBR Dam. This simulation used 11,200 virtual fish instead of the 8960 used for the best simulation.

Figure D.9 Vertical distribution of blueback herring as given by both actual and virtual hydroacoustic surveys. Instead of releasing fish uniformly throughout the lake as was done for the best simulation, this simulation released all fish near the upstream end of the lake.


Actual Survey
Virtual Survey
No Actual Survey Data Exists
r^2 = 0.92
Depth (m)
0
-2
-4
-6
-8
-10
-12
-14
-16
-18
-20
-22
-24
-26
-28
-30
-32
-34
-36
-38
0
5
10
15
20
25
% of Fish Sample Detected

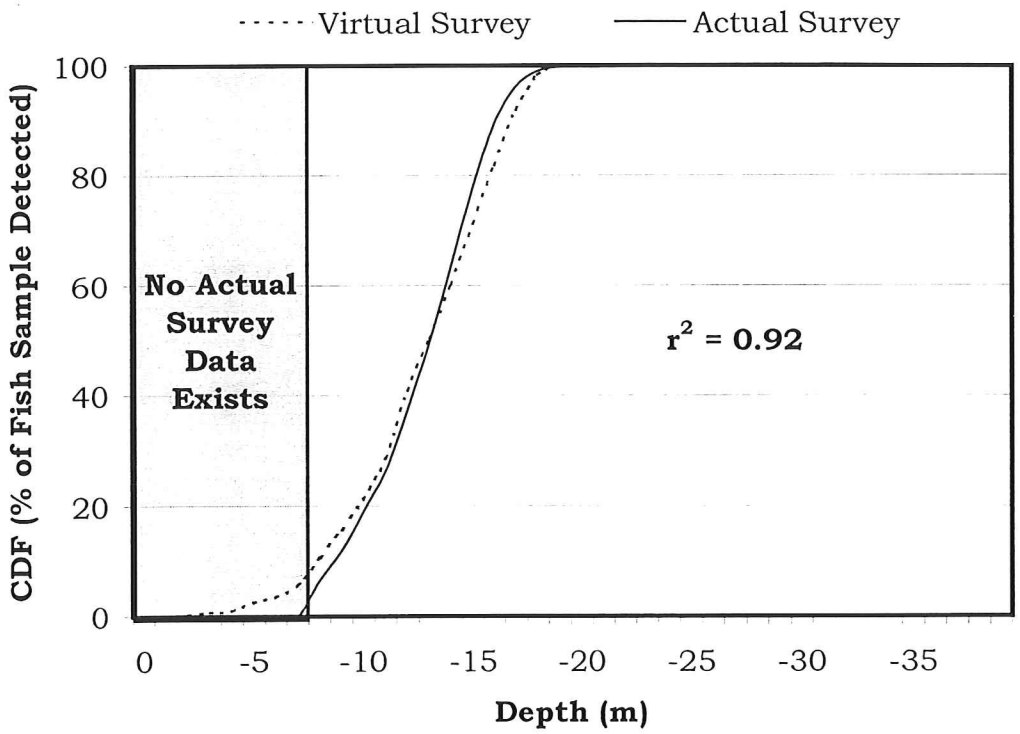


Figure D.10 Cumulative Distribution Function (CDF) showing the amount of the survey sample detected by depth. Instead of releasing fish uniformly throughout the lake as was done for the best simulation, this simulation released all fish near the upstream end of the lake.

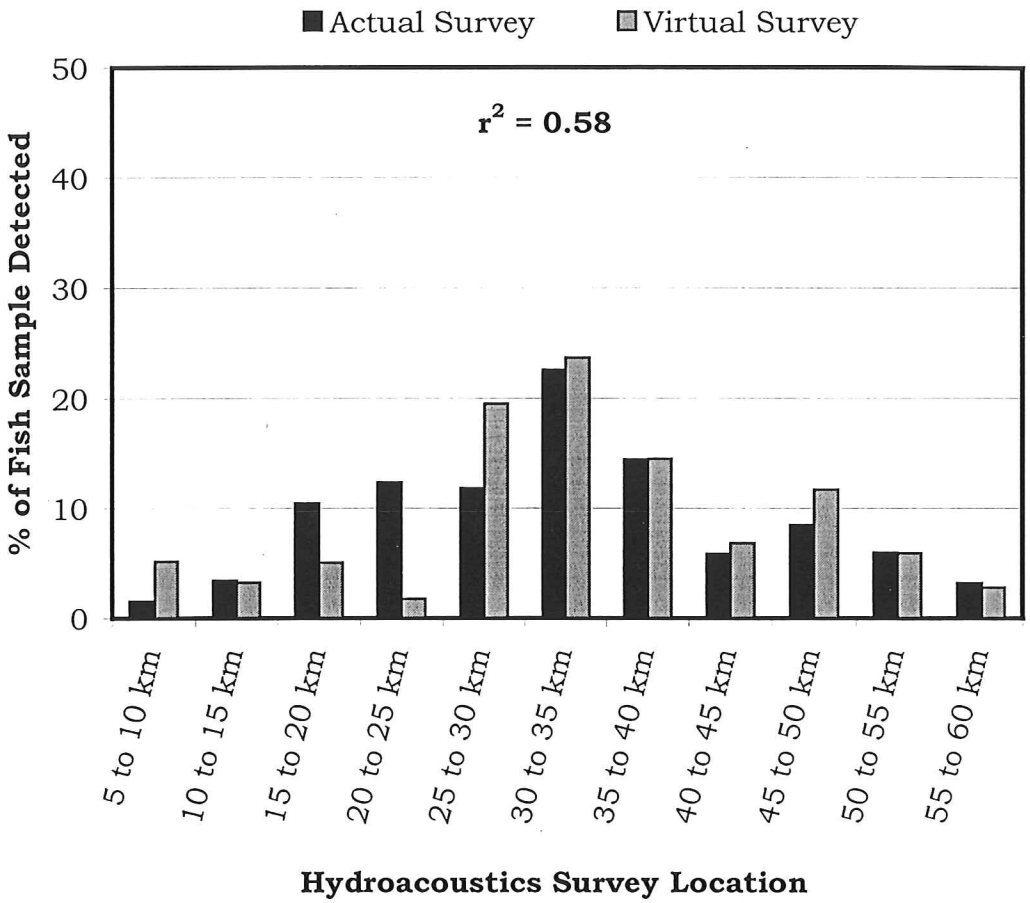


Figure D.11 Longitudinal distribution of blueback herring as given by both actual and virtual hydroacoustic surveys. Instead of releasing fish uniformly throughout the lake as was done for the best simulation, this simulation released all fish near the upstream end of the lake.

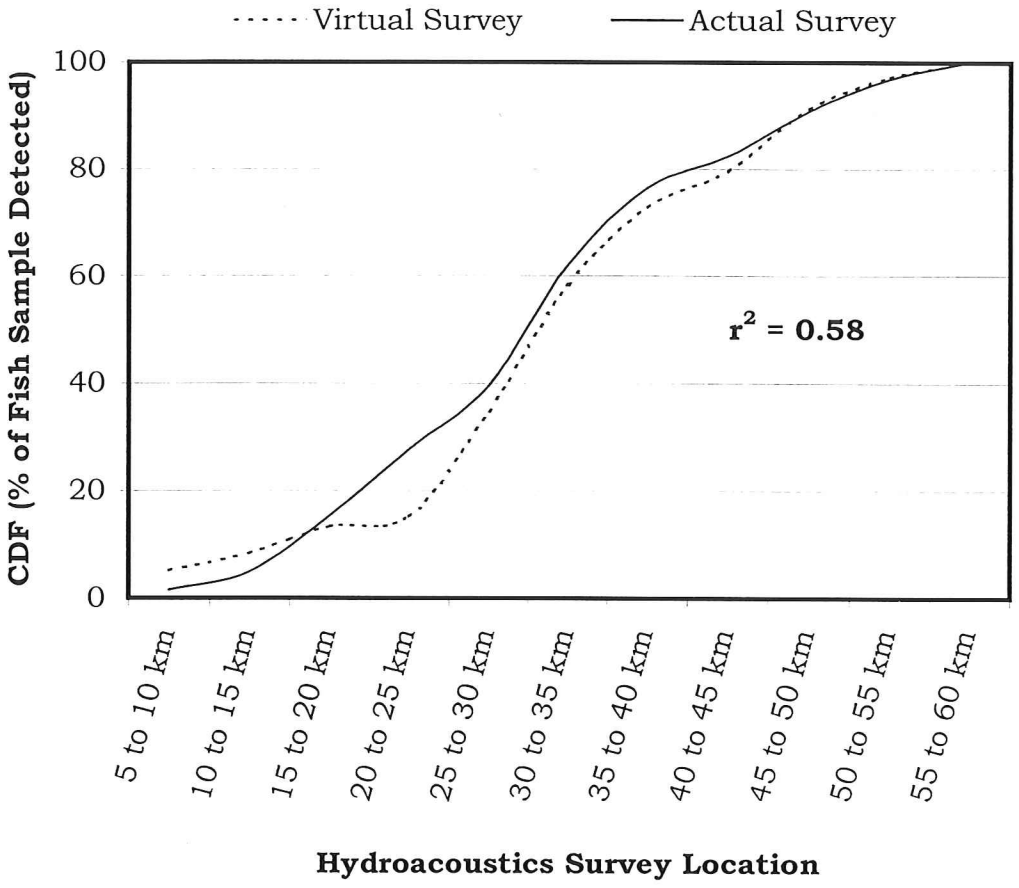
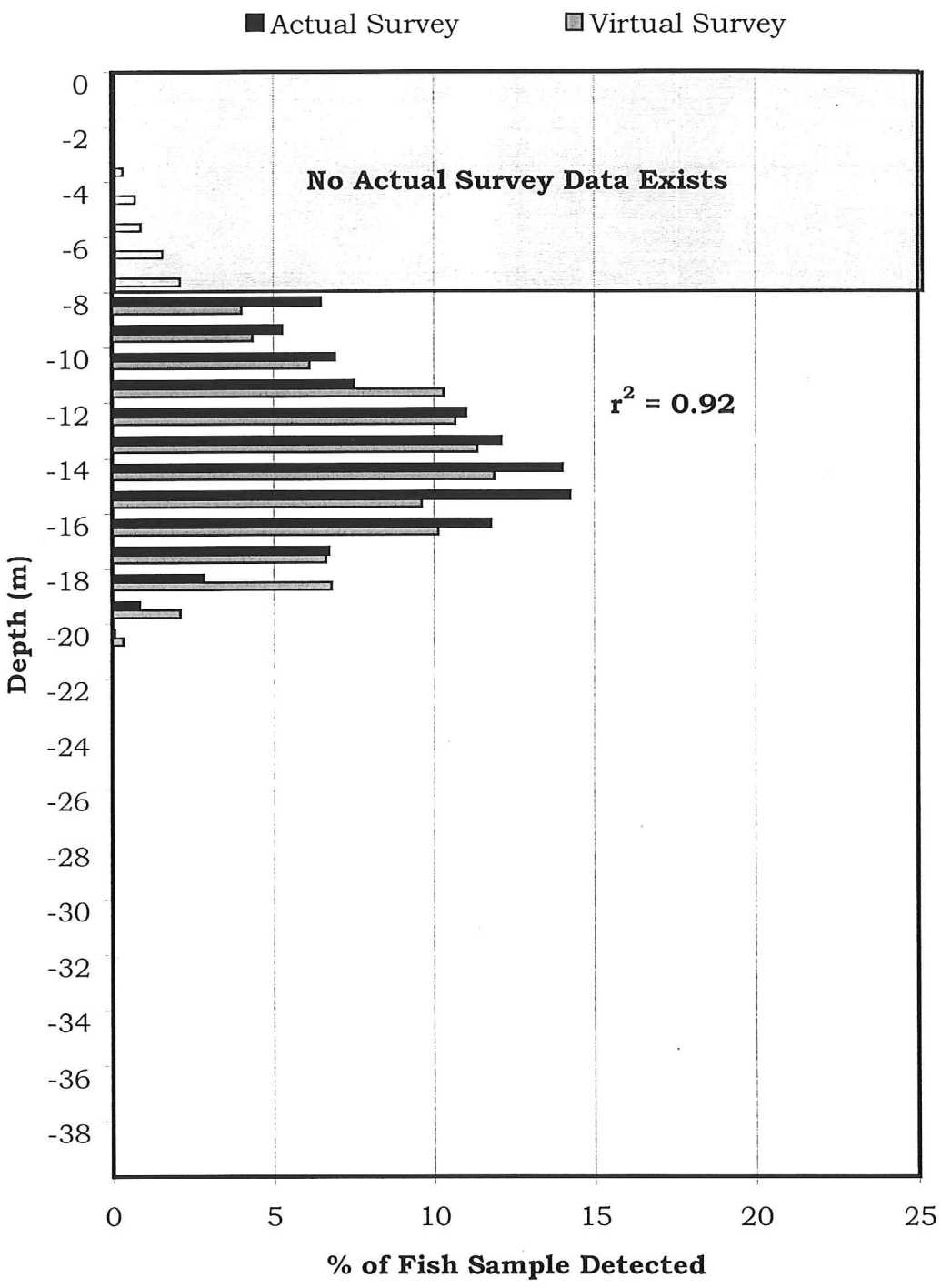


Figure D.12 Cumulative Distribution Function (CDF) showing the amount of the survey sample detected by distance downstream from RBR Dam. Instead of releasing fish uniformly throughout the lake as was done for the best simulation, this simulation released all fish near the upstream end of the lake.

Figure D.13 Vertical distribution of blueback herring as given by both actual and virtual hydroacoustic surveys. Instead of releasing fish uniformly throughout the lake as was done for the best simulation, this simulation released all fish near the middle of the lake.


Actual Survey
Virtual Survey
No Actual Survey Data Exists
r^2 = 0.92
Depth (m)
0
-2
-4
-6
-8
-10
-12
-14
-16
-18
-20
-22
-24
-26
-28
-30
-32
-34
-36
-38
0
5
10
15
20
25
% of Fish Sample Detected

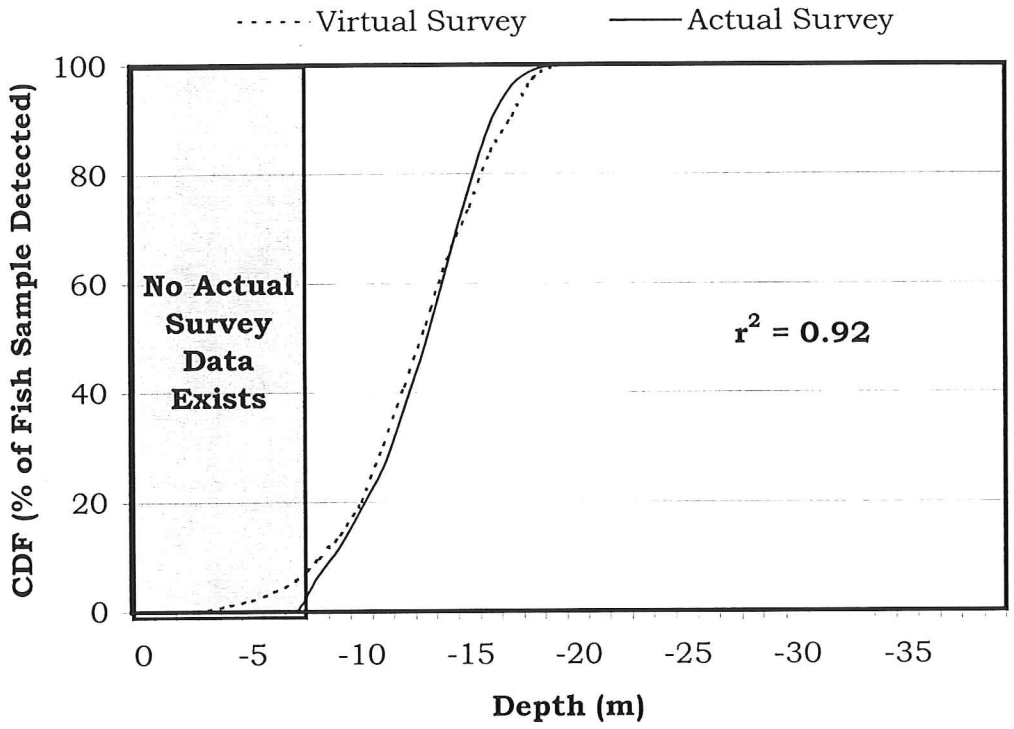


Figure D.14 Cumulative Distribution Function (CDF) showing the amount of the survey sample detected by depth. Instead of releasing fish uniformly throughout the lake as was done for the best simulation, this simulation released all fish near the middle of the lake.

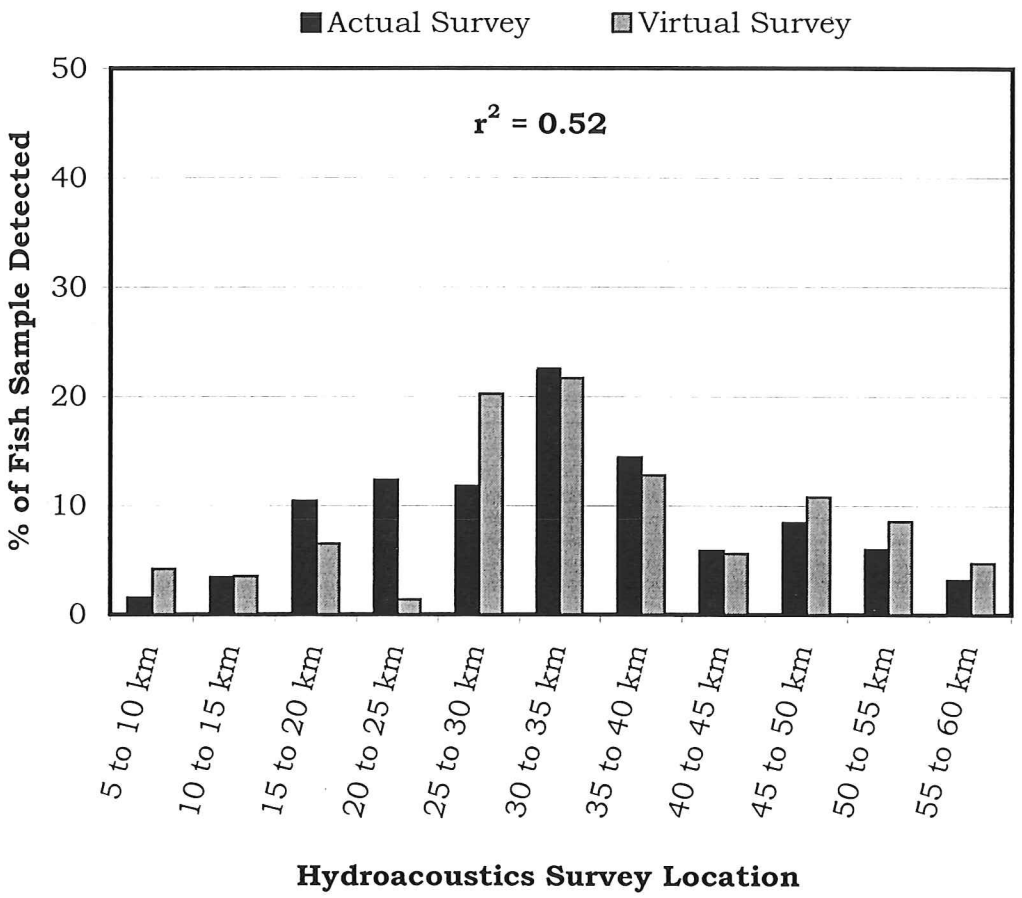


Figure D.15 Longitudinal distribution of blueback herring as given by both actual and virtual hydroacoustic surveys. Instead of releasing fish uniformly throughout the lake as was done for the best simulation, this simulation released all fish near the middle of the lake.

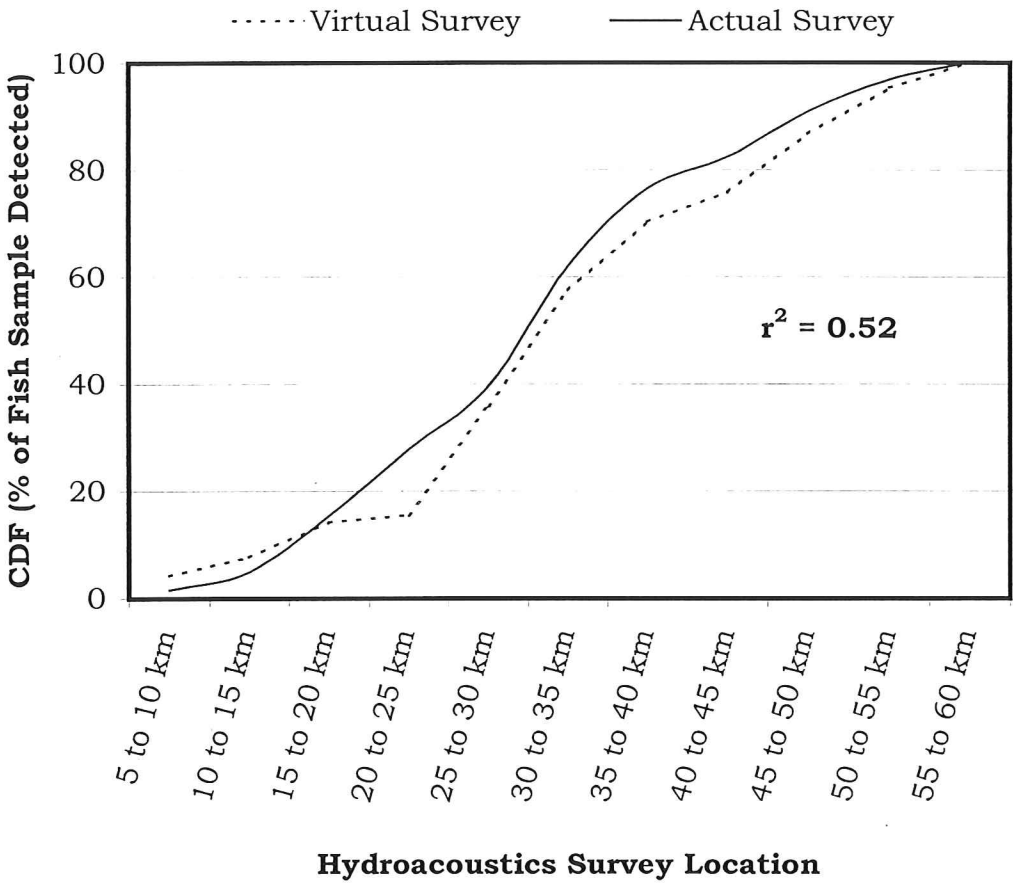
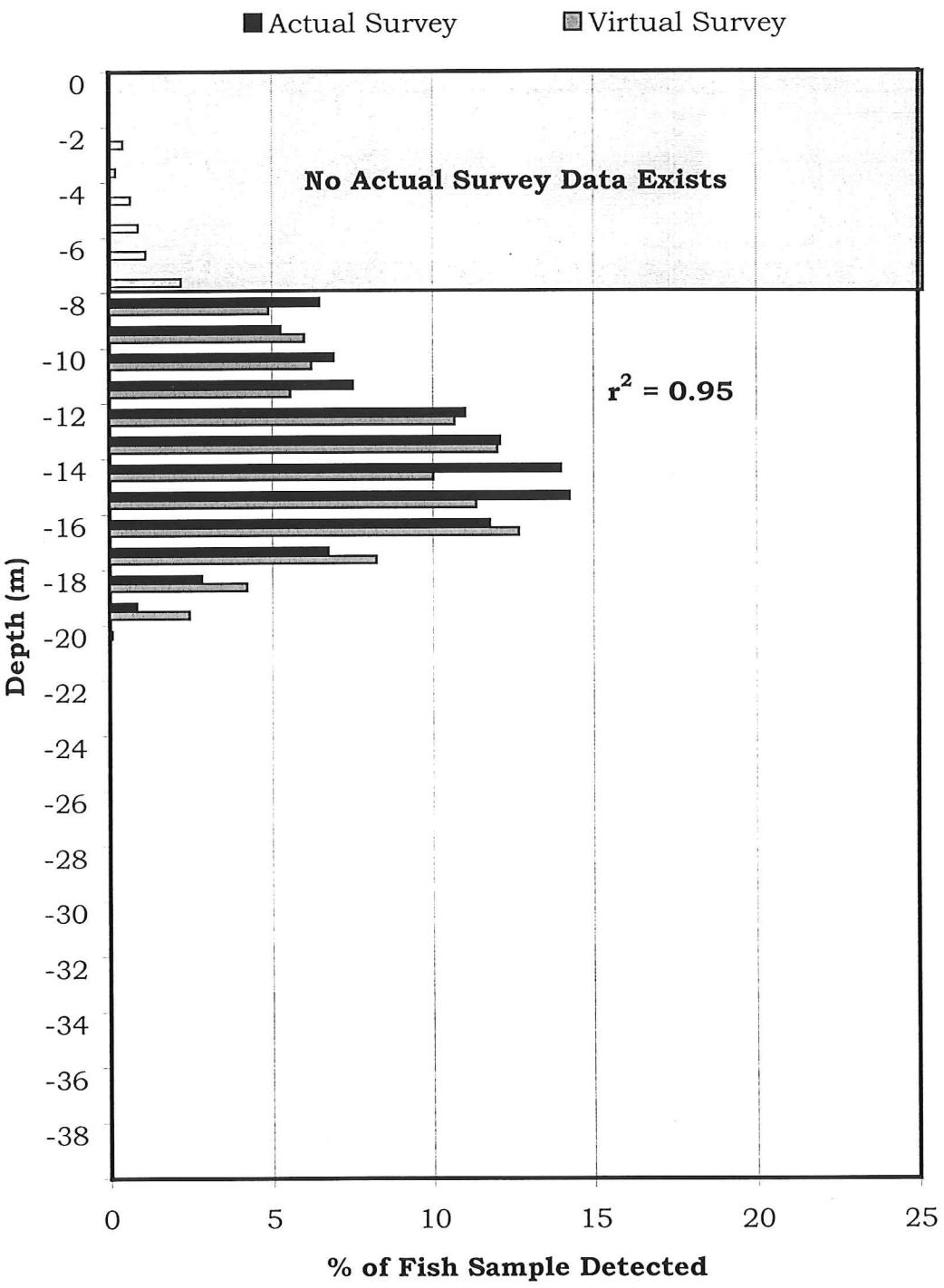


Figure D.16 Cumulative Distribution Function (CDF) showing the amount of the survey sample detected by distance downstream from RBR Dam. Instead of releasing fish uniformly throughout the lake as was done for the best simulation, this simulation released all fish near the middle of the lake.

Figure D.17 Vertical distribution of blueback herring as given by both actual and virtual hydroacoustic surveys. This simulation released fish on March 31st (JDAY 91), as opposed to the best simulation, which released fish on May 1st (JDAY 122).


Actual Survey
Virtual Survey
No Actual Survey Data Exists
r^2 = 0.95
Depth (m)
0
-2
-4
-6
-8
-10
-12
-14
-16
-18
-20
-22
-24
-26
-28
-30
-32
-34
-36
-38
0
5
10
15
20
25
% of Fish Sample Detected

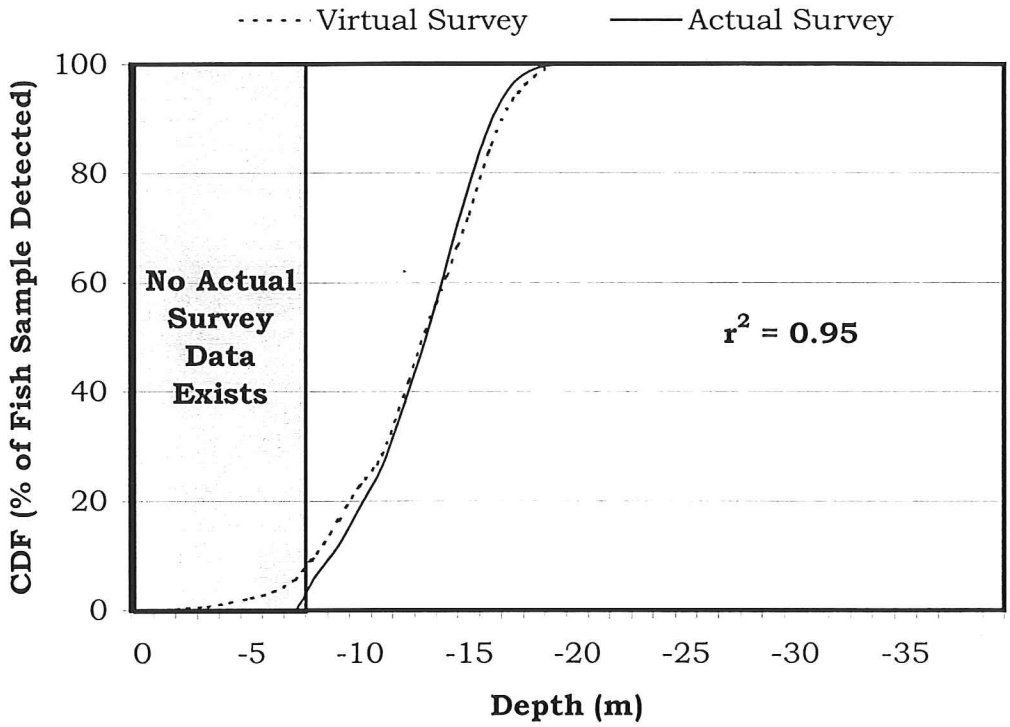


Figure D.18 Cumulative Distribution Function (CDF) showing the amount of the survey sample detected by depth. This simulation released fish on March 31st (JDAY 91), as opposed to the best simulation, which released fish on May 1st (JDAY 122).

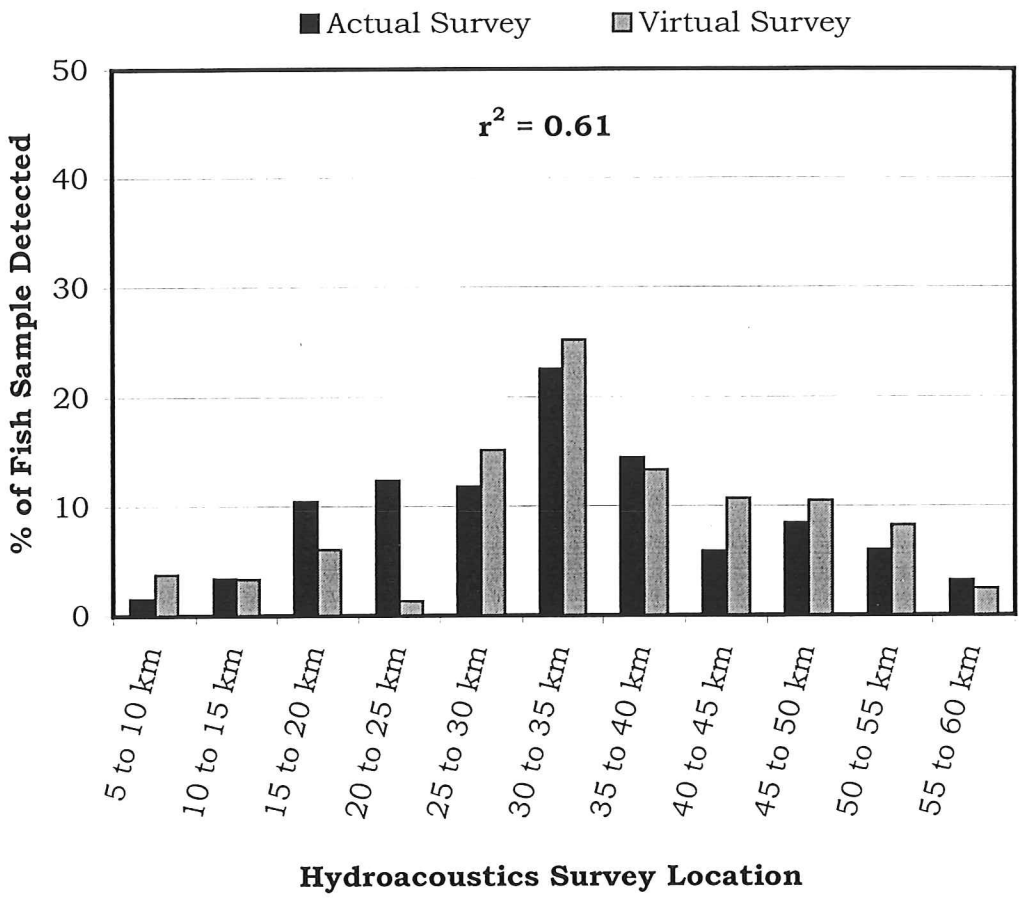


Figure D.19 Longitudinal distribution of blueback herring as given by both actual and virtual hydroacoustic surveys. This simulation released fish on March 31st (JDAY 91), as opposed to the best simulation, which released fish on May 1st (JDAY 122).

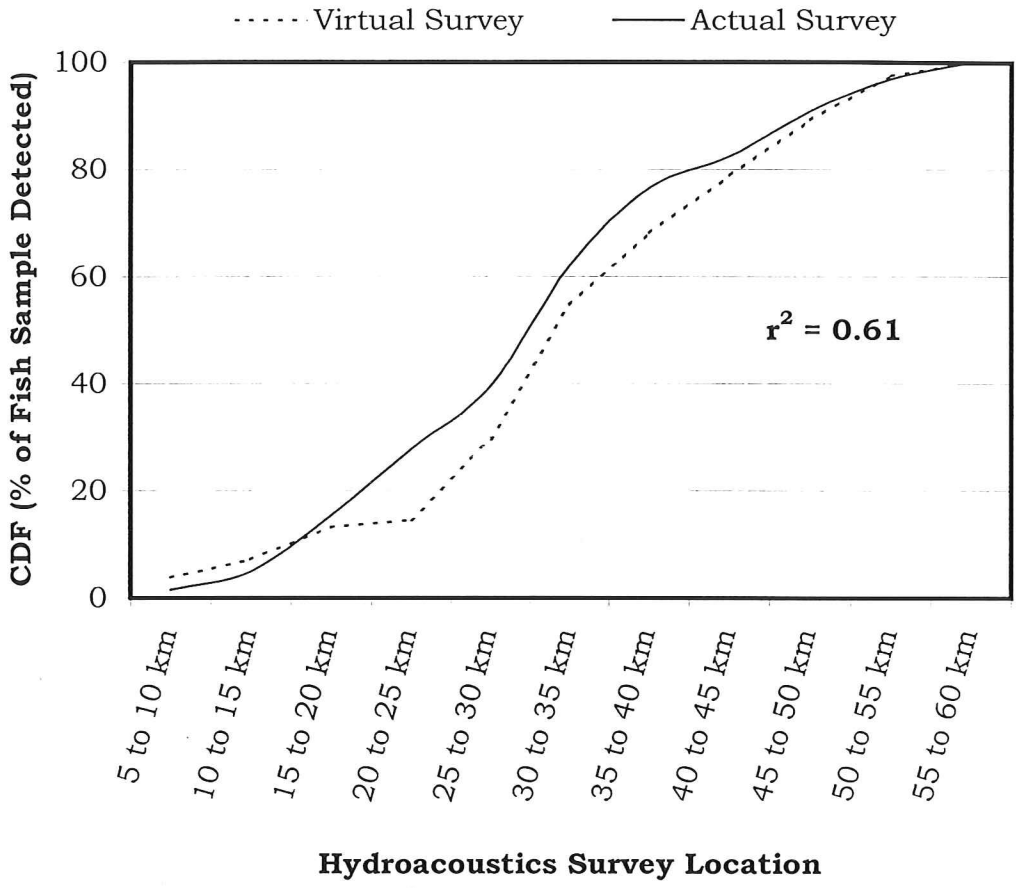
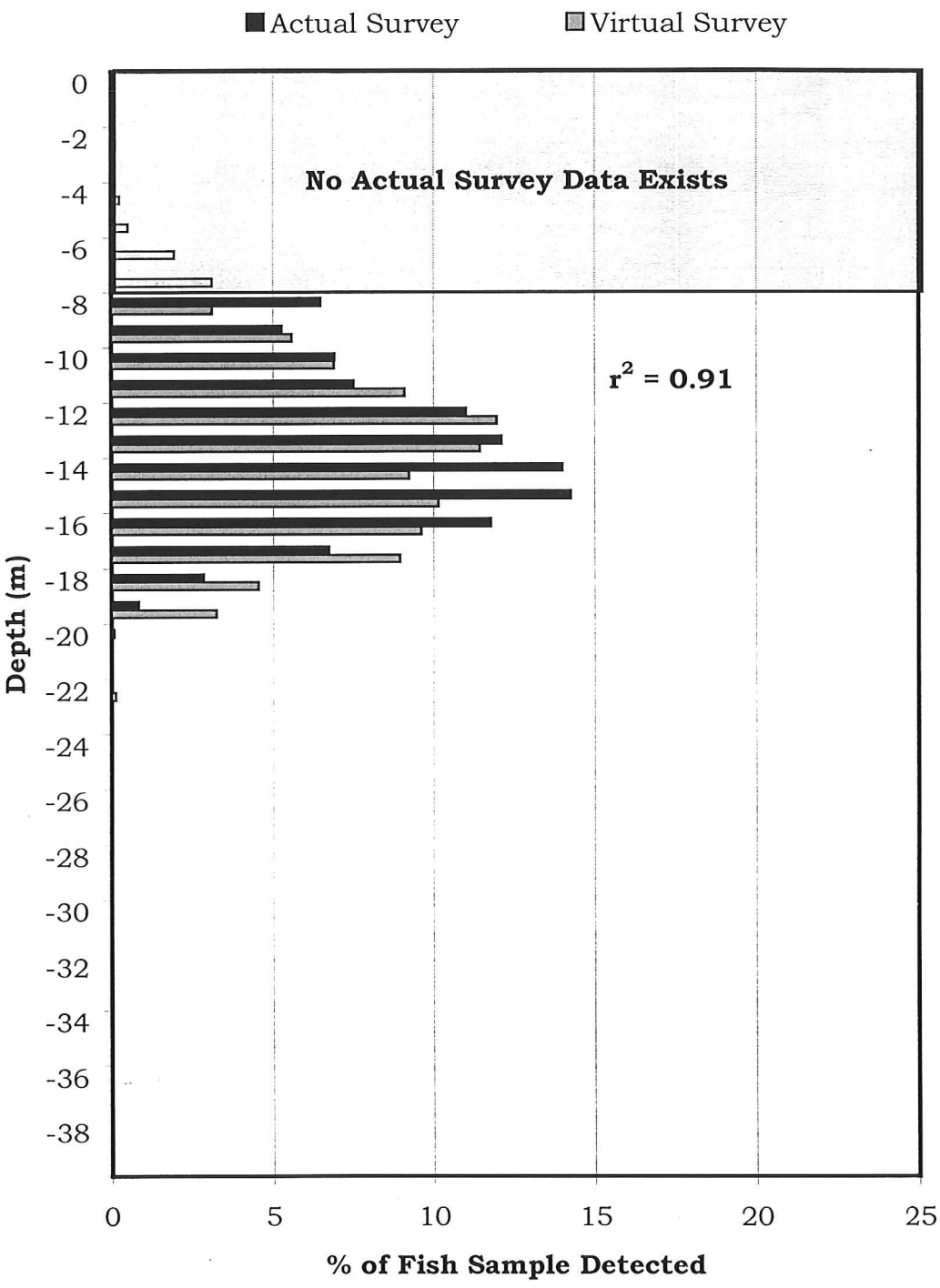


Figure D.20 Cumulative Distribution Function (CDF) showing the amount of the survey sample detected by distance downstream from RBR Dam. This simulation released fish on March 31st (JDAY 91), as opposed to the best simulation, which released fish on May 1st (JDAY 122).

Figure D.21 Vertical distribution of blueback herring as given by both actual and virtual hydroacoustic surveys. This simulation released fish on June 1st (JDAY 153), as opposed to the best simulation, which released fish on May 1st (JDAY 122).


Actual Survey
Virtual Survey
No Actual Survey Data Exists
r^2 = 0.91
Depth (m)
0
-2
-4
-6
-8
-10
-12
-14
-16
-18
-20
-22
-24
-26
-28
-30
-32
-34
-36
-38
0
5
10
15
20
25
% of Fish Sample Detected

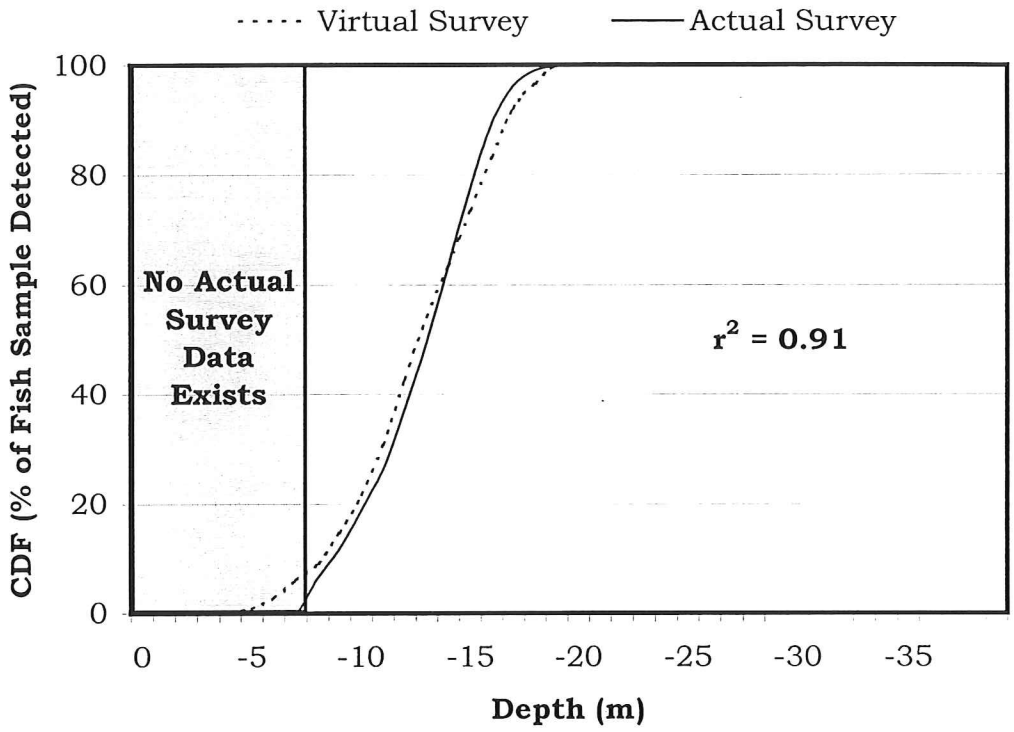


Figure D.22 Cumulative Distribution Function (CDF) showing the amount of the survey sample detected by depth. This simulation released fish on June 1st (JDAY 153), as opposed to the best simulation, which released fish on May 1st (JDAY 122).

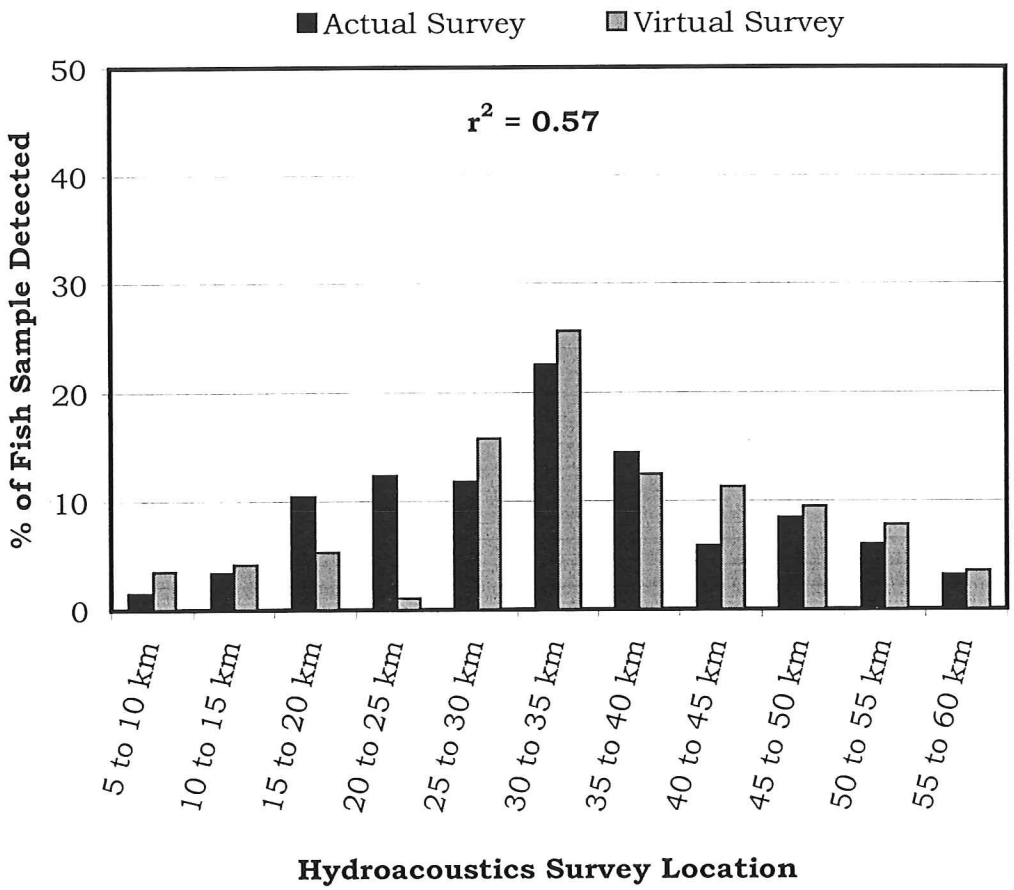


Figure D.23 Longitudinal distribution of blueback herring as given by both actual and virtual hydroacoustic surveys. This simulation released fish on June 1st (JDAY 153), as opposed to the best simulation, which released fish on May 1st (JDAY 122).

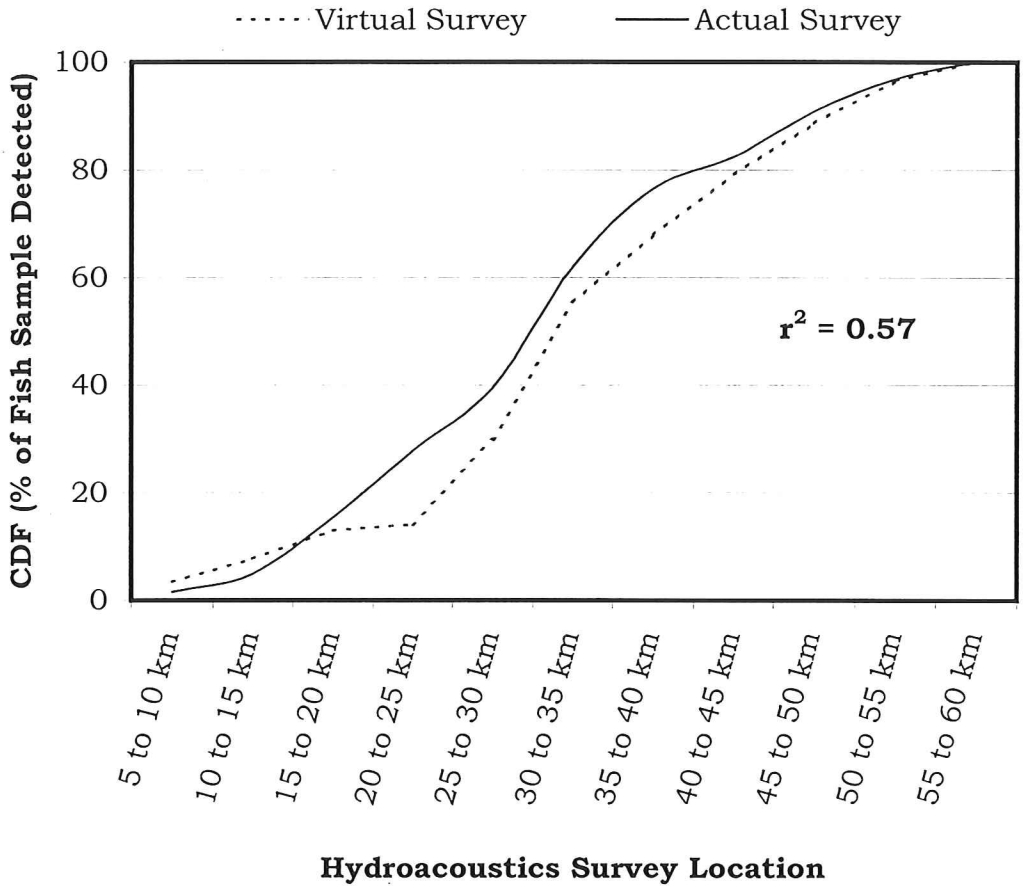
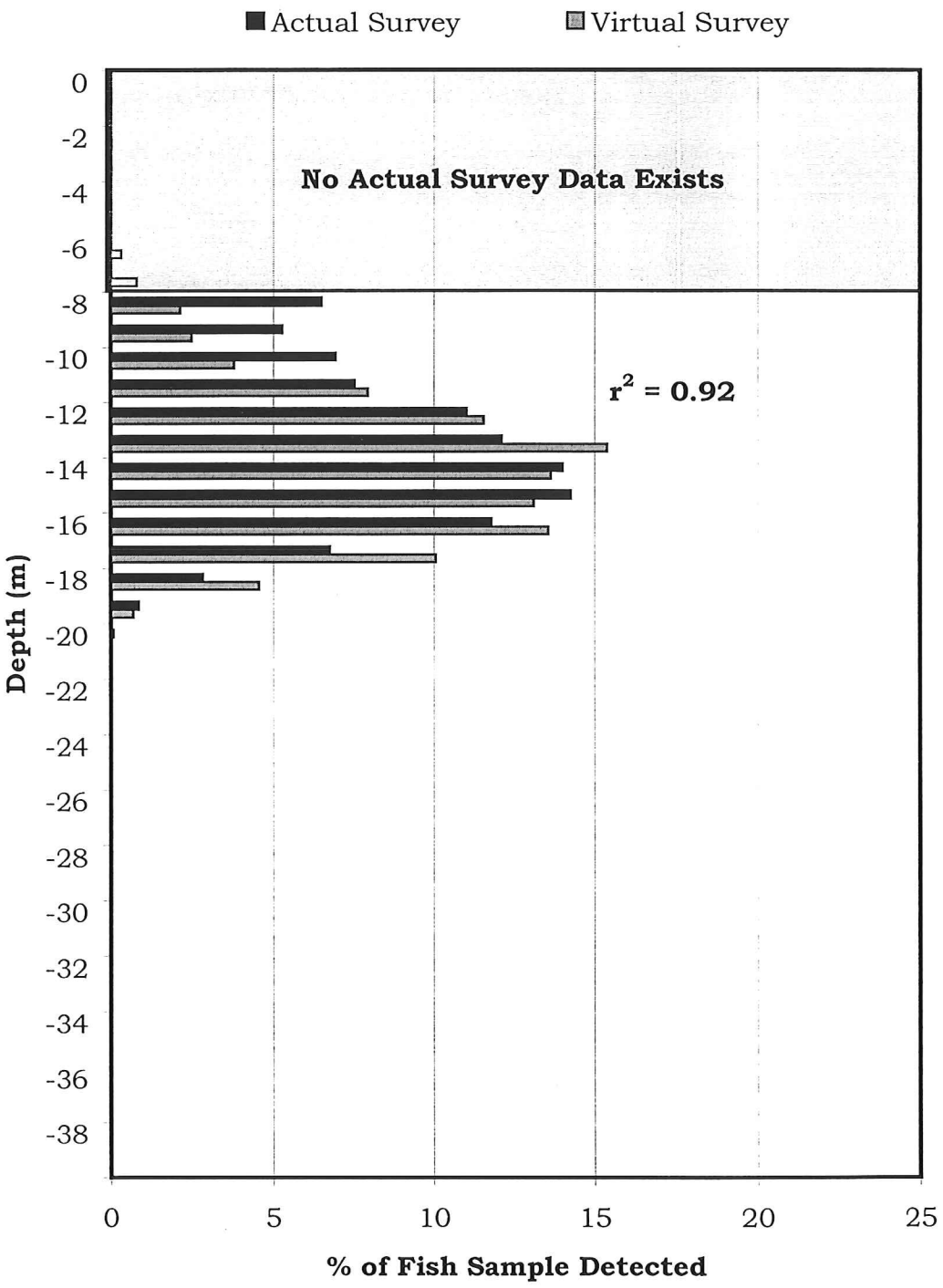


Figure D.24 Cumulative Distribution Function (CDF) showing the amount of the survey sample detected by distance downstream from RBR Dam. This simulation released fish on June 1st (JDAY 153), as opposed to the best simulation, which released fish on May 1st (JDAY 122).

Figure D.25 Vertical distribution of blueback herring as given by both actual and virtual hydroacoustic surveys. This simulation used a NFS time step averaging 5 min, as opposed to the best simulation, which used a NFS time step averaging 9 min.


Actual Survey
Virtual Survey
No Actual Survey Data Exists
r^2 = 0.92
Depth (m)
0
-2
-4
-6
-8
-10
-12
-14
-16
-18
-20
-22
-24
-26
-28
-30
-32
-34
-36
-38
0
5
10
15
20
25
% of Fish Sample Detected

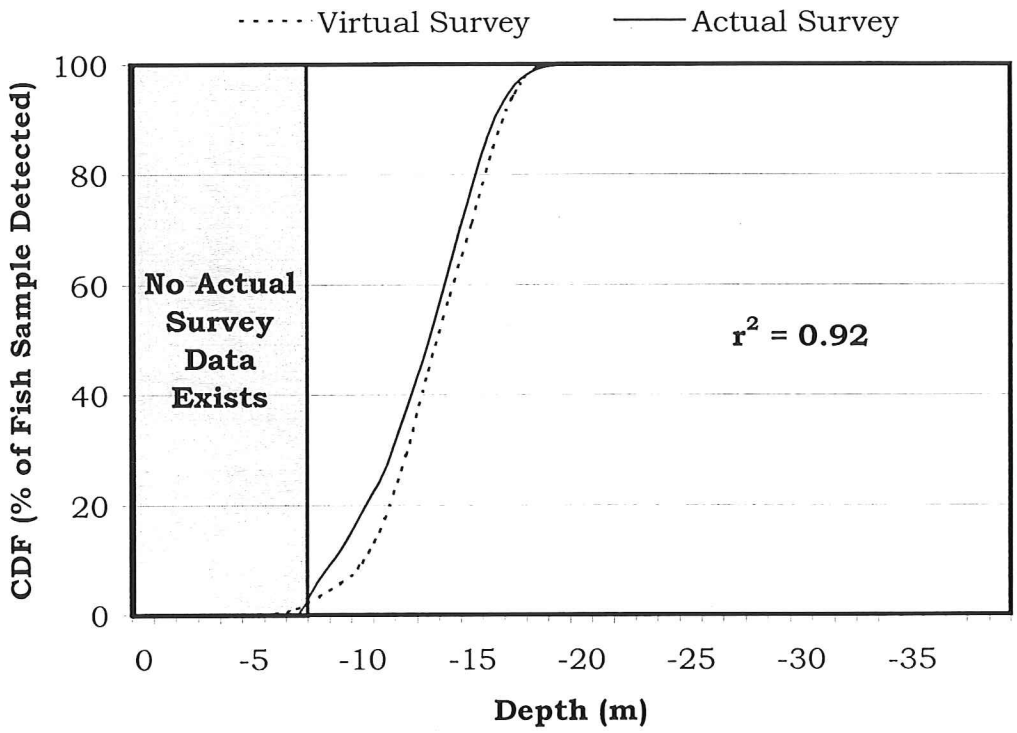


Figure D.26 Cumulative Distribution Function (CDF) showing the amount of the survey sample detected by depth. This simulation used a NFS time step averaging 5 min, as opposed to the best simulation, which used a NFS time step averaging 9 min.

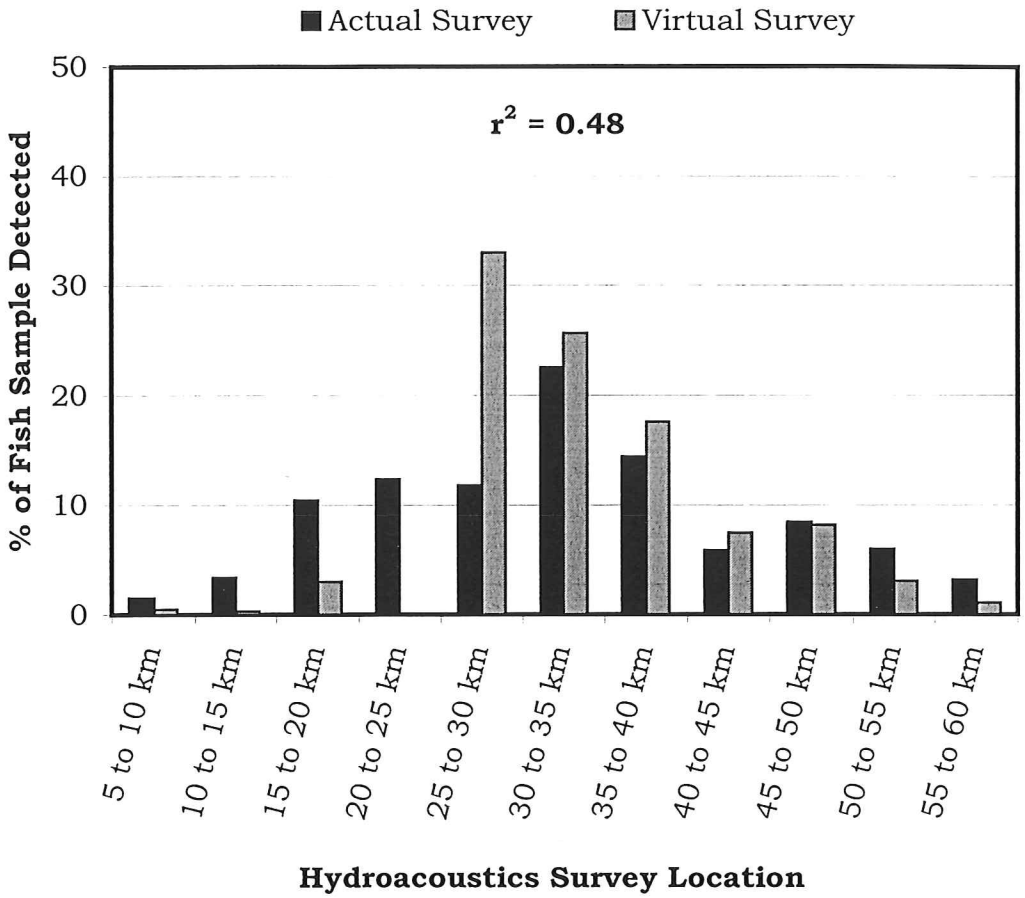


Figure D.27 Longitudinal distribution of blueback herring as given by both actual and virtual hydroacoustic surveys. This simulation used a NFS time step averaging 5 min, as opposed to the best simulation, which used a NFS time step averaging 9 min.

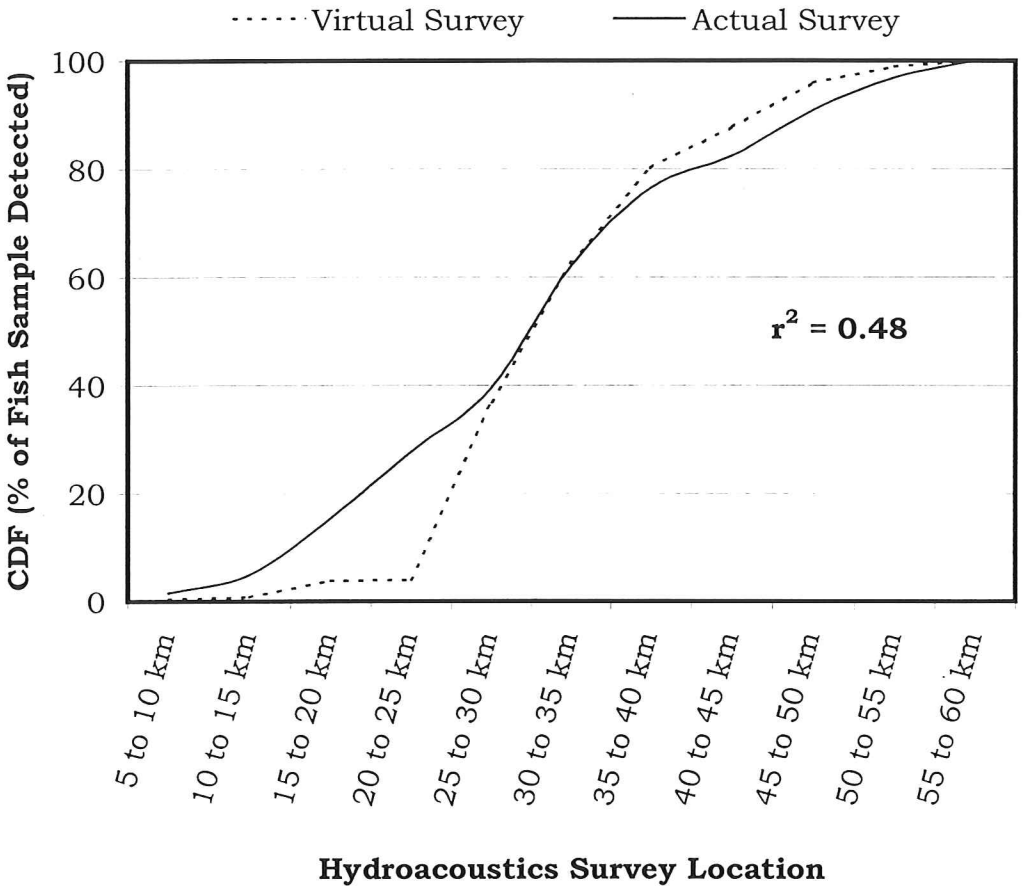
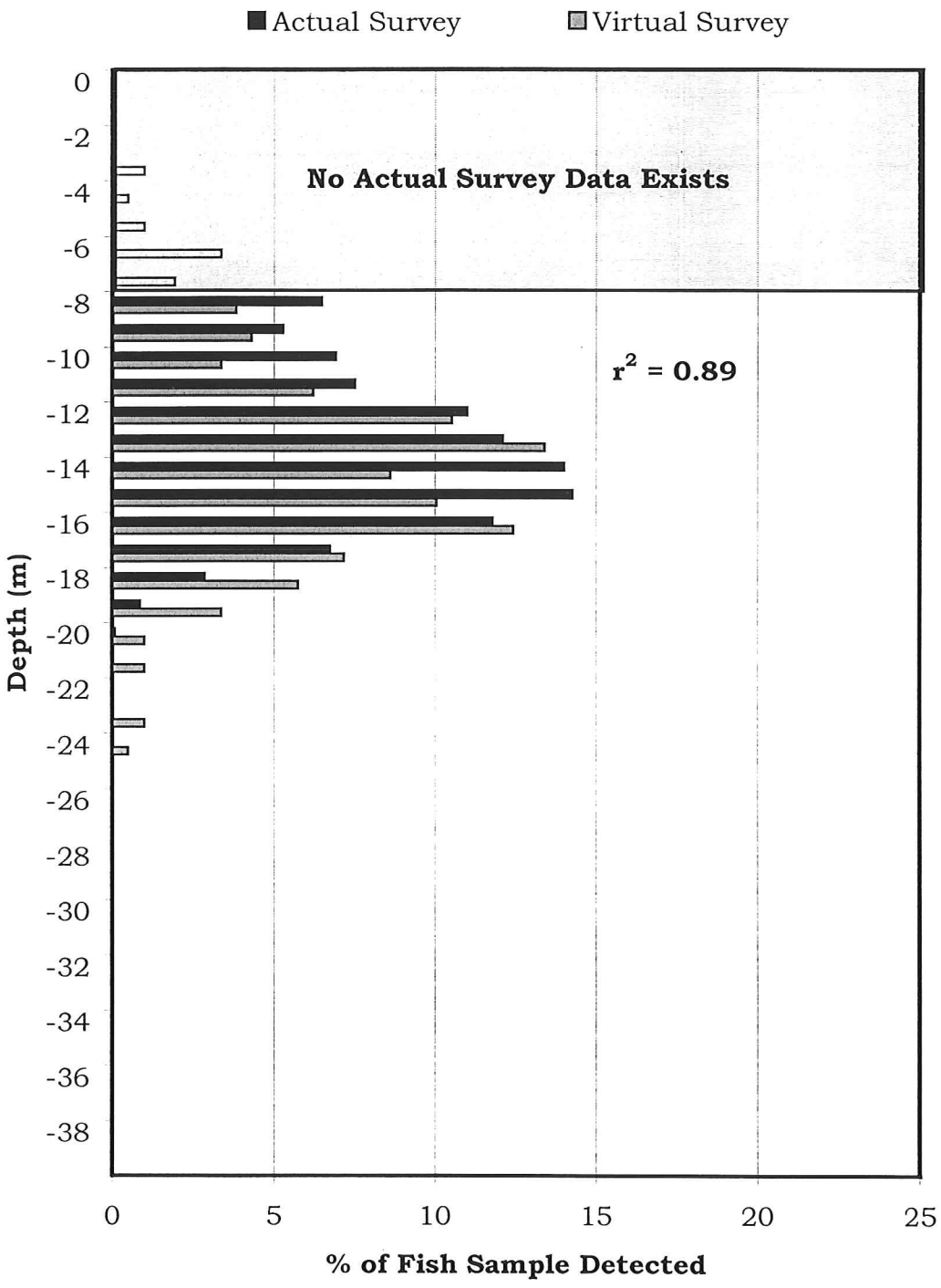


Figure D.28 Cumulative Distribution Function (CDF) showing the amount of the survey sample detected by distance downstream from RBR Dam. This simulation used a NFS time step averaging 5 min, as opposed to the best simulation, which used a NFS time step averaging 9 min.

Figure D.29 Vertical distribution of blueback herring as given by both actual and virtual hydroacoustic surveys. This simulation used a NFS time step averaging 15 min, as opposed to the best simulation, which used a NFS time step averaging 9 min.


Actual Survey
Virtual Survey
No Actual Survey Data Exists
r^2 = 0.89
Depth (m)
0
-2
-4
-6
-8
-10
-12
-14
-16
-18
-20
-22
-24
-26
-28
-30
-32
-34
-36
-38
0
5
10
15
20
25
% of Fish Sample Detected

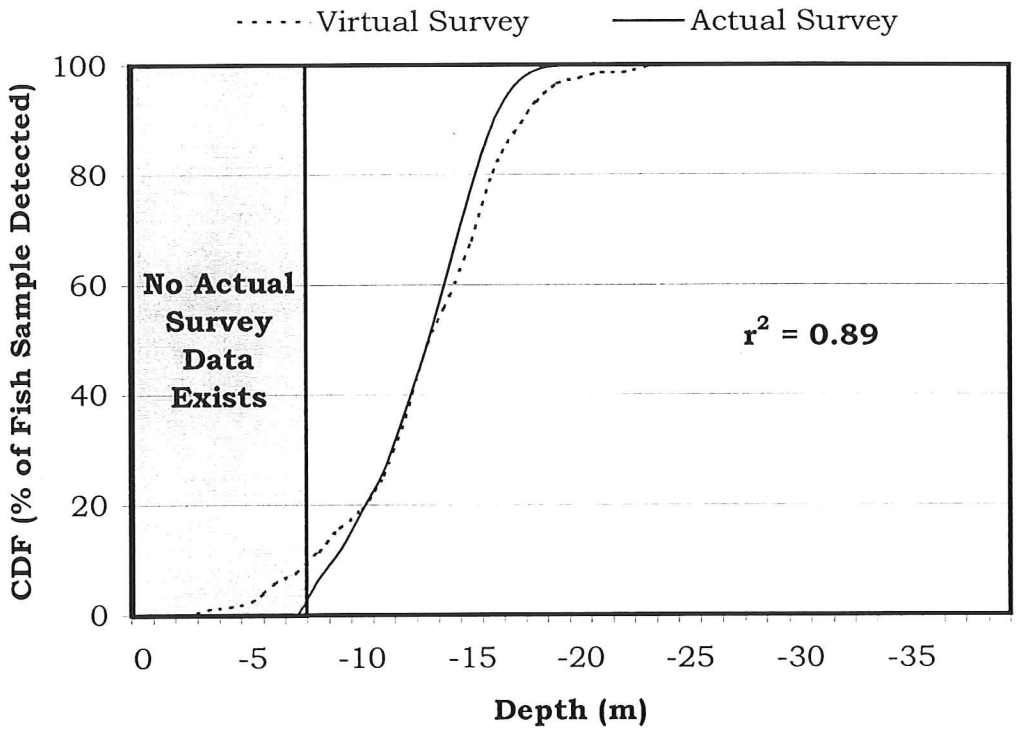


Figure D.30 Cumulative Distribution Function (CDF) showing the amount of the survey sample detected by depth. This simulation used a NFS time step averaging 15 min, as opposed to the best simulation, which used a NFS time step averaging 9 min.

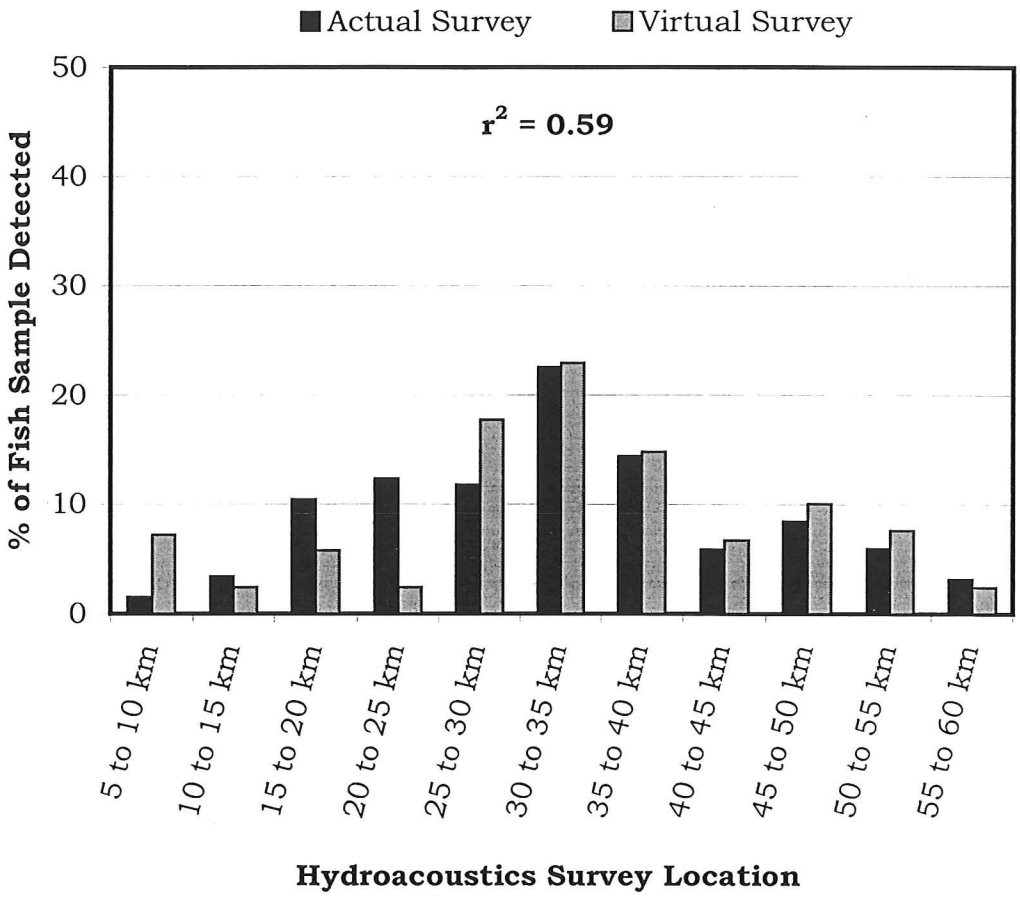


Figure D.31 Longitudinal distribution of blueback herring as given by both actual and virtual hydroacoustic surveys. This simulation used a NFS time step averaging 15 min, as opposed to the best simulation, which used a NFS time step averaging 9 min.

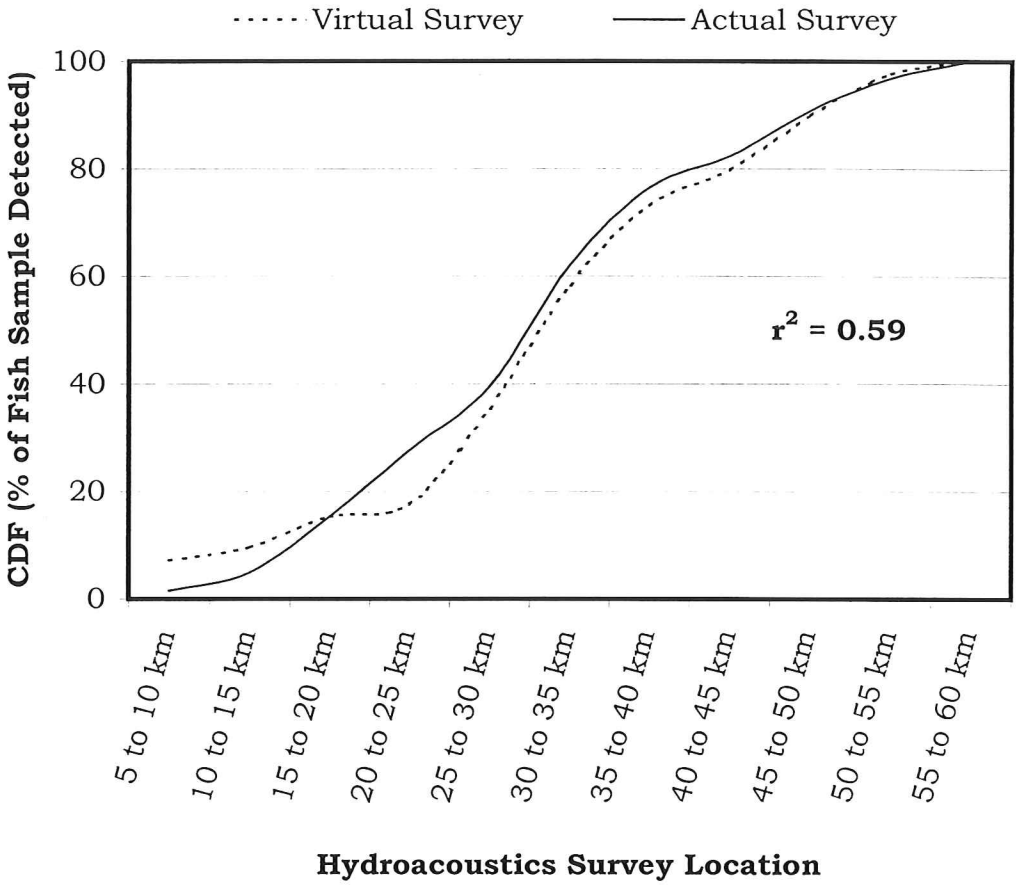
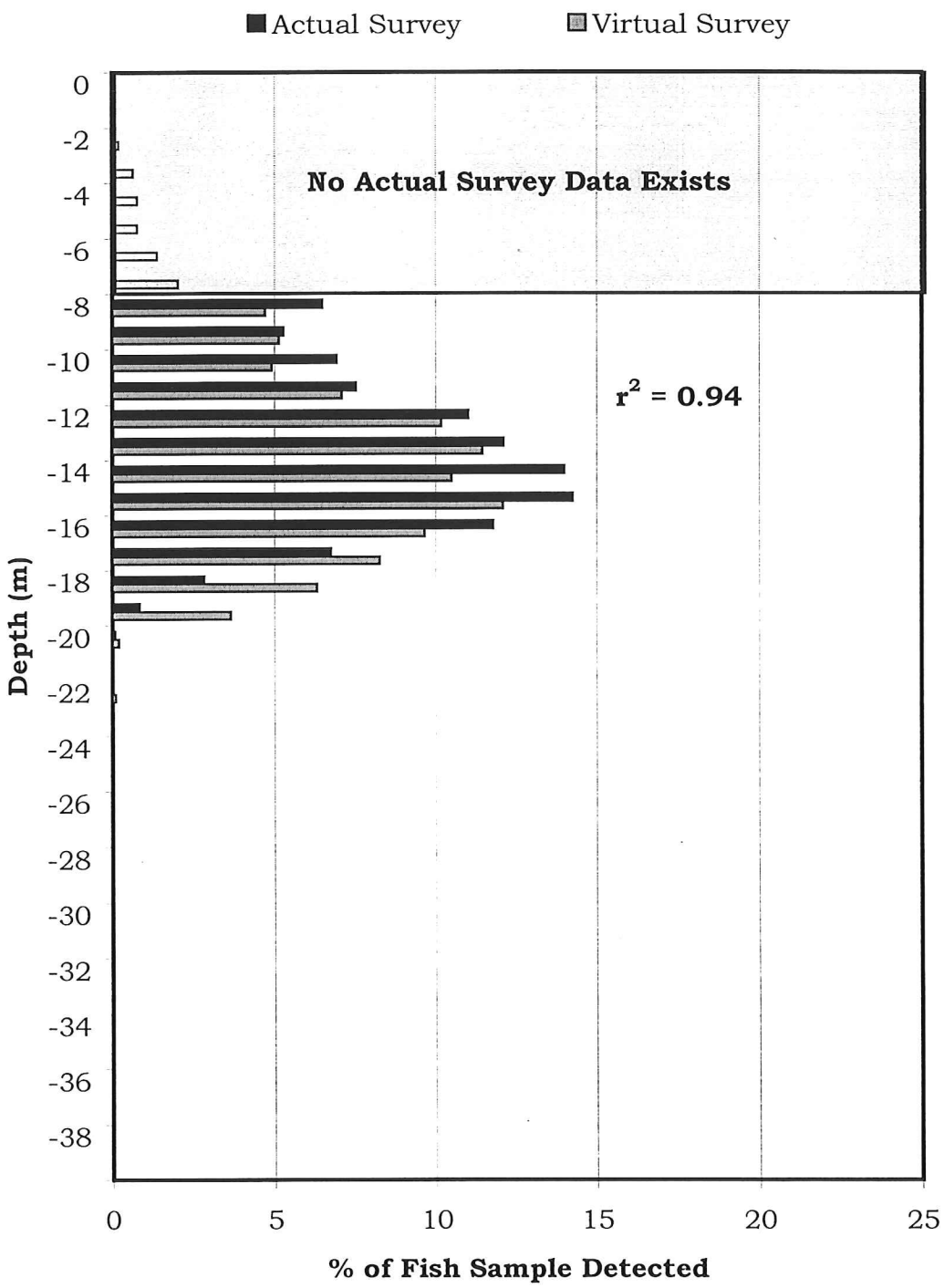


Figure D.32 Cumulative Distribution Function (CDF) showing the amount of the survey sample detected by distance downstream from RBR Dam. This simulation used a NFS time step averaging 15 min, as opposed to the best simulation, which used a NFS time step averaging 9 min.

Figure D.33 Vertical distribution of blueback herring as given by both actual and virtual hydroacoustic surveys. This simulation used weights for responding to horizontal velocity stimuli that were 20% stronger than the weights used to obtain the best simulation.


Actual Survey
Virtual Survey
No Actual Survey Data Exists
r^2 = 0.94
Depth (m)
0
-2
-4
-6
-8
-10
-12
-14
-16
-18
-20
-22
-24
-26
-28
-30
-32
-34
-36
-38
0
5
10
15
20
25
% of Fish Sample Detected

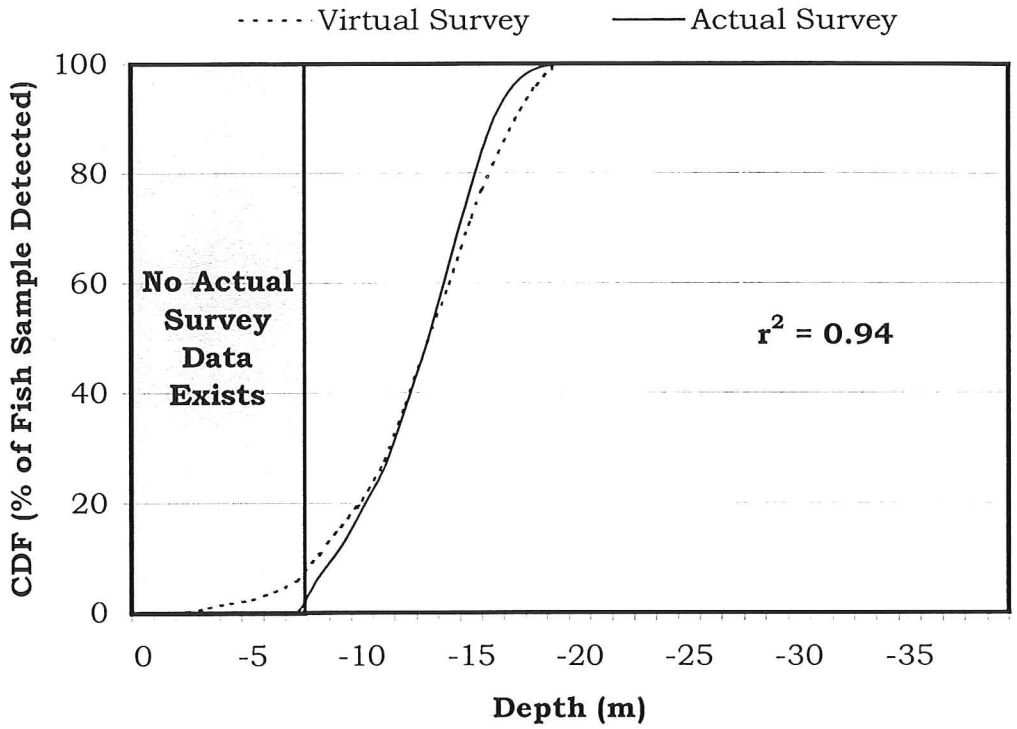


Figure D.34 Cumulative Distribution Function (CDF) showing the amount of the survey sample detected by depth. This simulation used weights for responding to horizontal velocity stimuli that were 20% stronger than the weights used to obtain the best simulation.

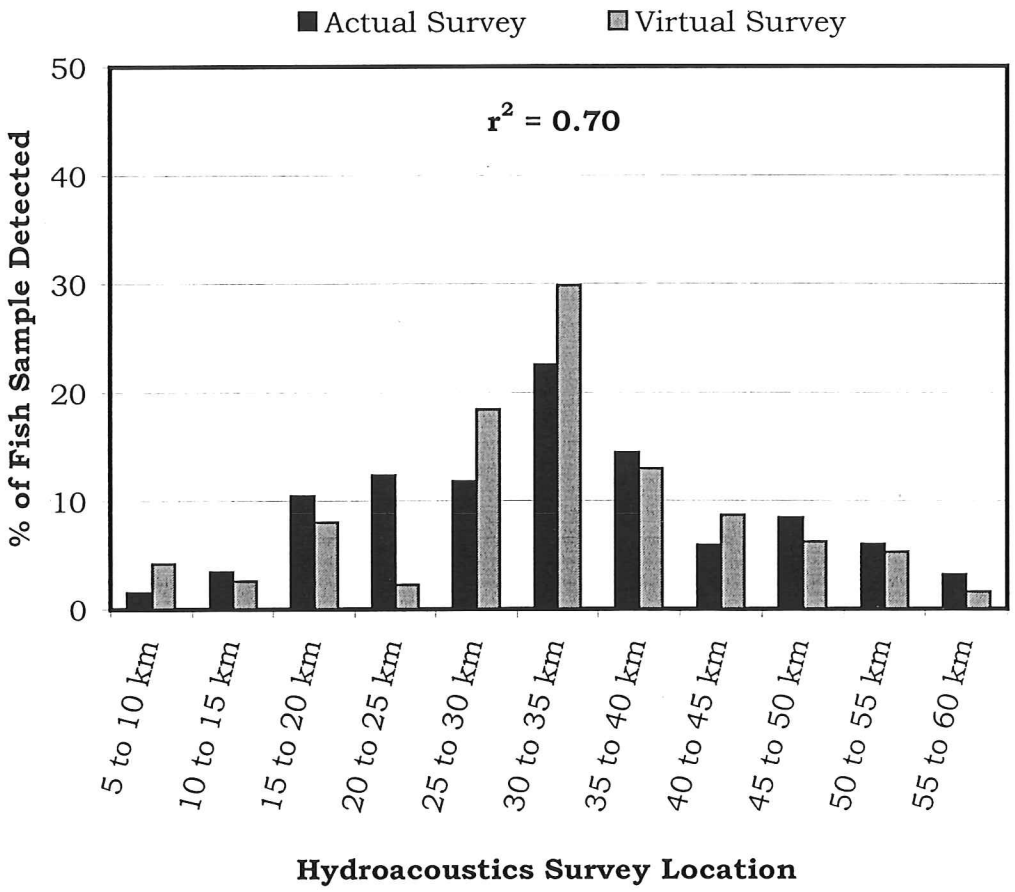


Figure D.35 Longitudinal distribution of blueback herring as given by both actual and virtual hydroacoustic surveys. This simulation used weights for responding to horizontal velocity stimuli that were 20% stronger than the weights used to obtain the best simulation.

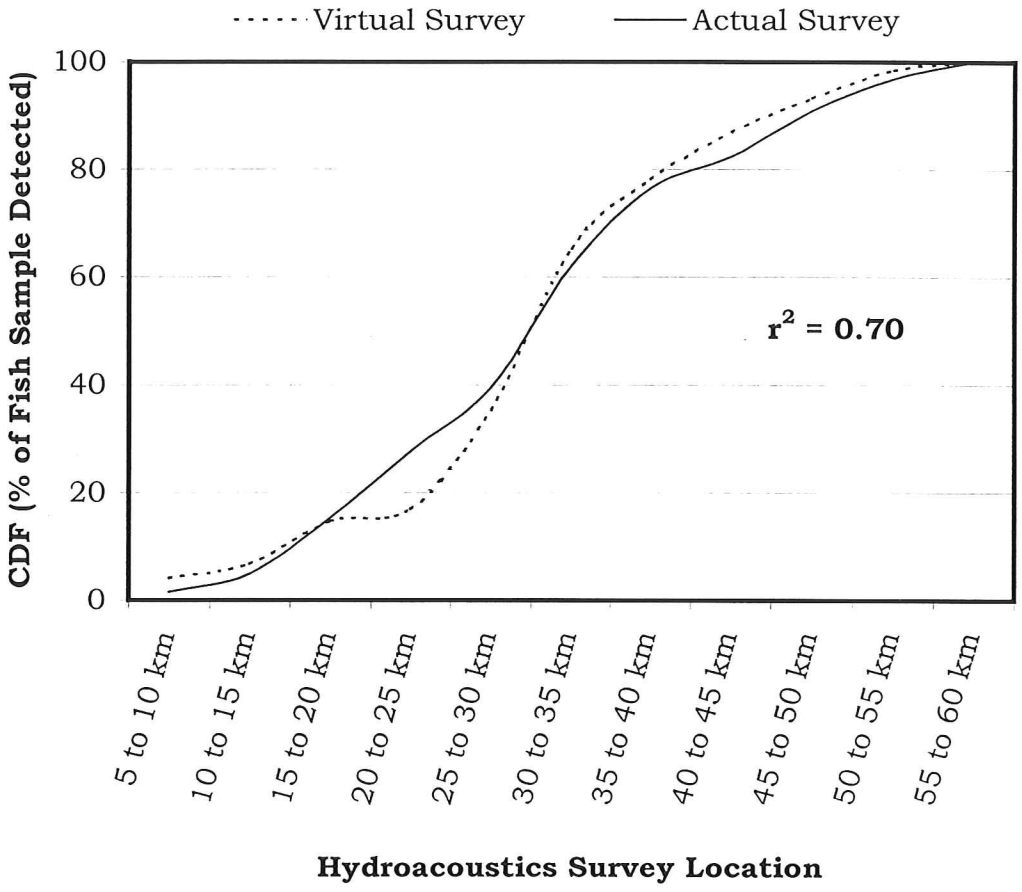
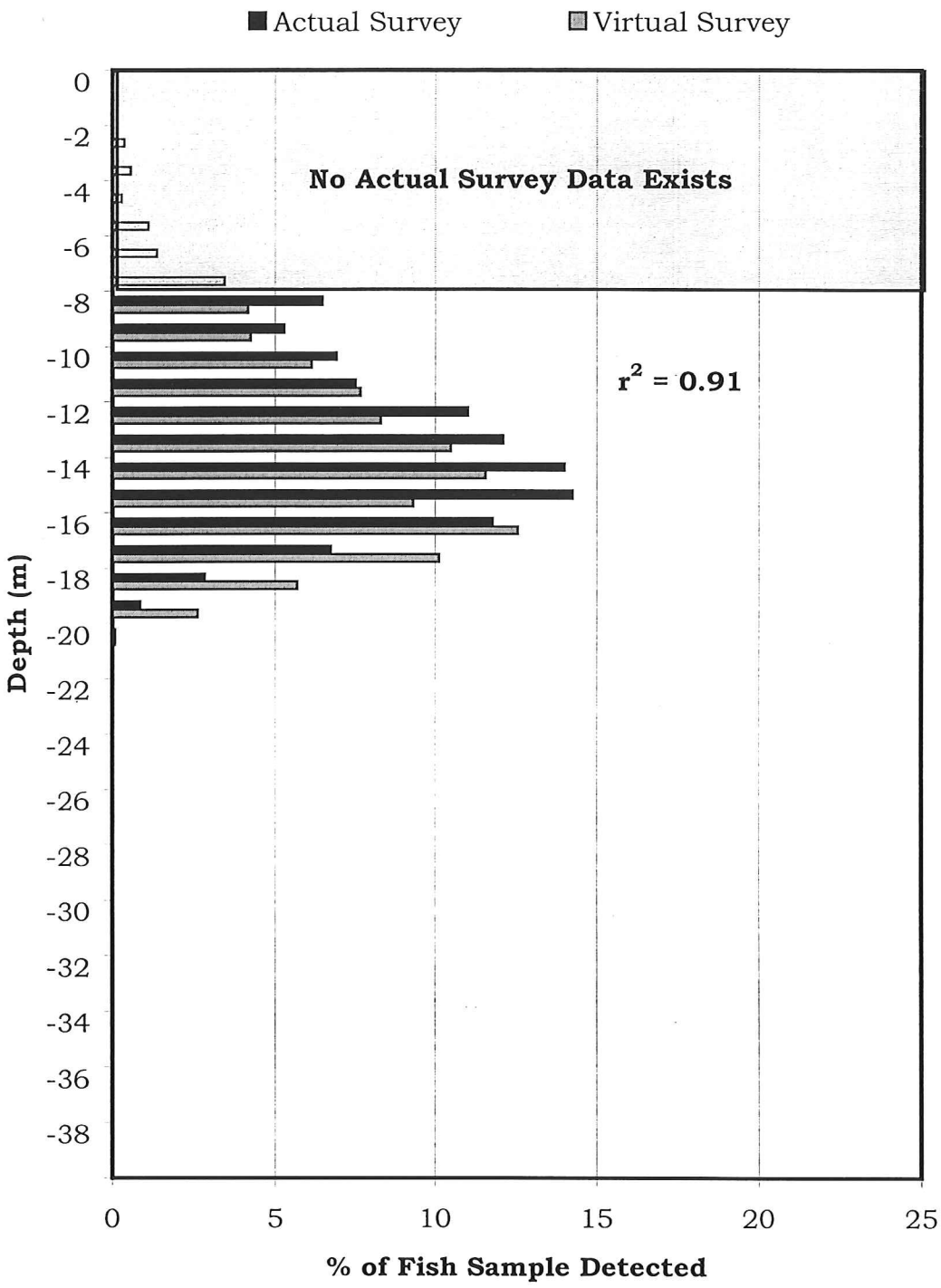


Figure D.36 Cumulative Distribution Function (CDF) showing the amount of the survey sample detected by distance downstream from RBR Dam. This simulation used weights for responding to horizontal velocity stimuli that were 20% stronger than the weights used to obtain the best simulation.

Figure D.37 Vertical distribution of blueback herring as given by both actual and virtual hydroacoustic surveys. This simulation used weights for responding to temperature stimuli that were 30% weaker than the weights used to obtain the best simulation.


Actual Survey
Virtual Survey
No Actual Survey Data Exists
r^2 = 0.91
Depth (m)
0
-2
-4
-6
-8
-10
-12
-14
-16
-18
-20
-22
-24
-26
-28
-30
-32
-34
-36
-38
0
5
10
15
20
25
% of Fish Sample Detected

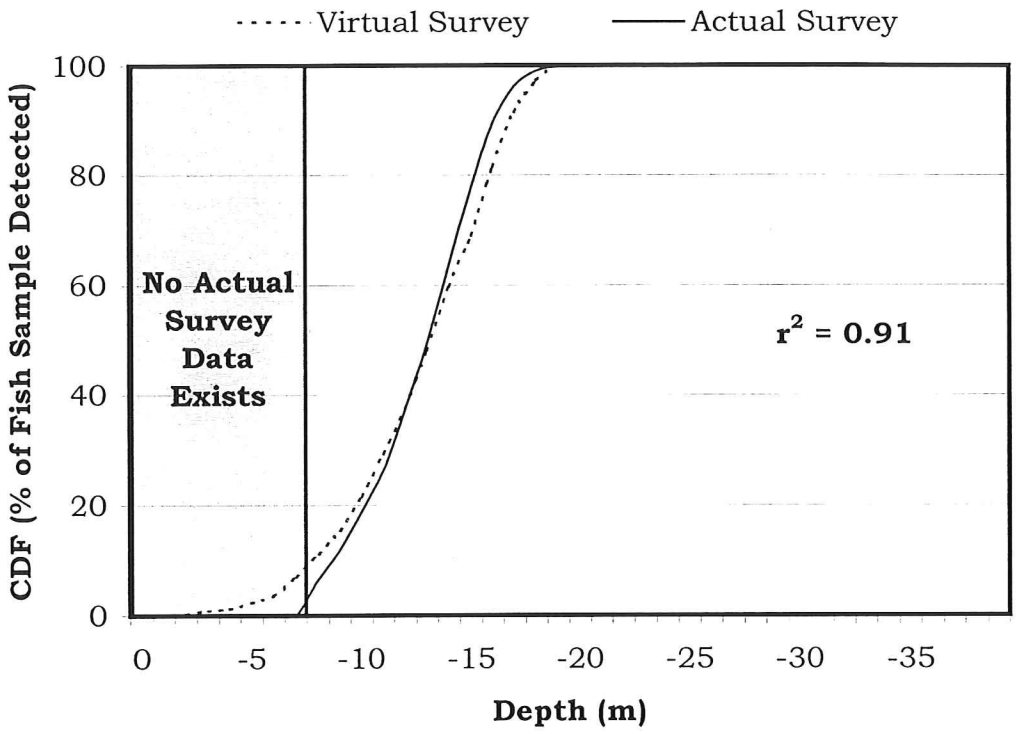


Figure D.38 Cumulative Distribution Function (CDF) showing the amount of the survey sample detected by depth. This simulation used weights for responding to temperature stimuli that were 30% weaker than the weights used to obtain the best simulation.

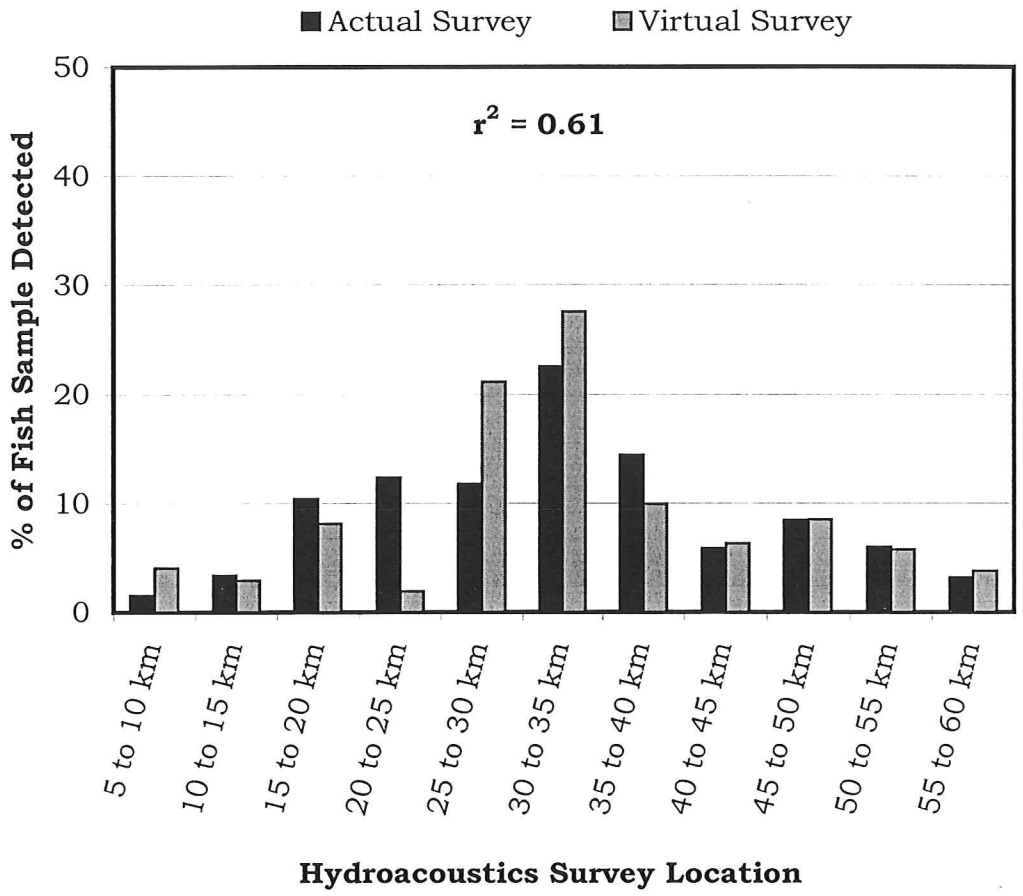


Figure D.39 Longitudinal distribution of blueback herring as given by both actual and virtual hydroacoustic surveys. This simulation used weights for responding to temperature stimuli that were 30% weaker than the weights used to obtain the best simulation.

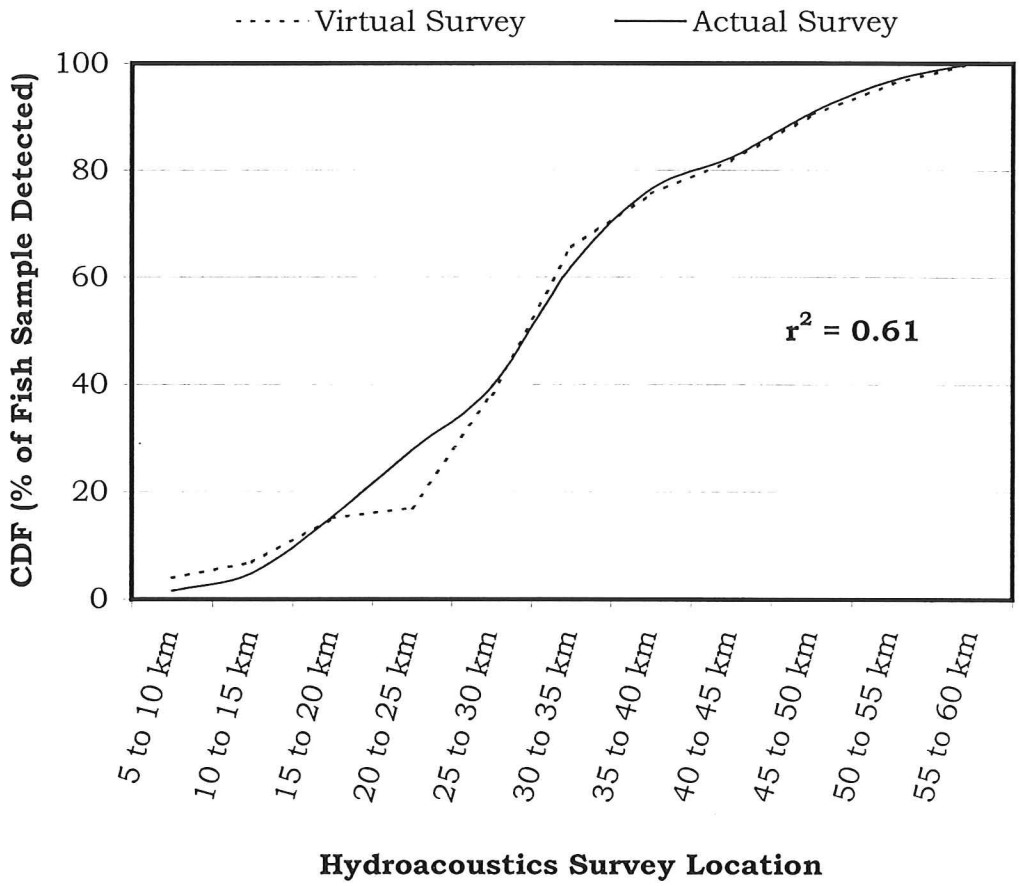
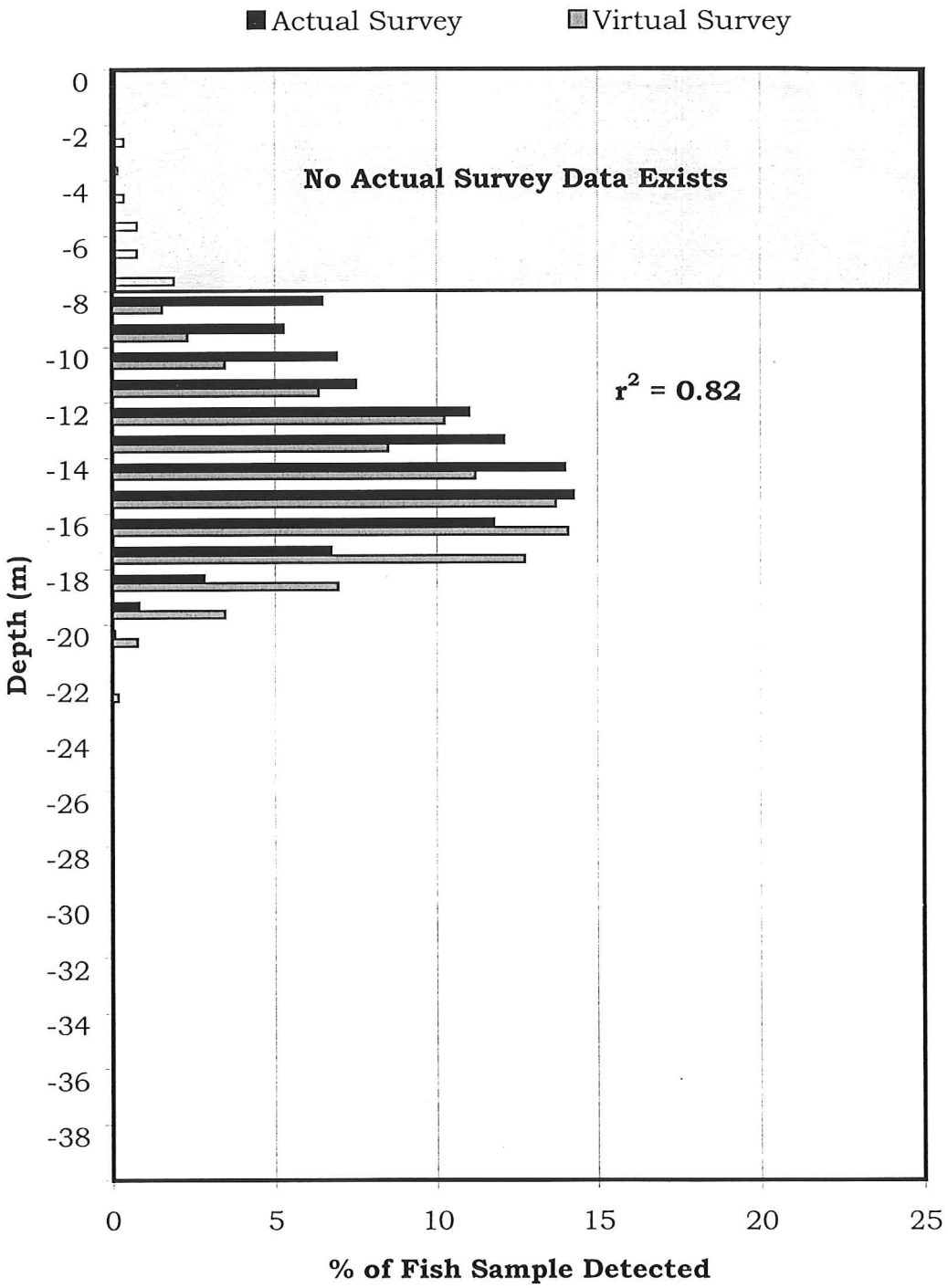


Figure D.40 Cumulative Distribution Function (CDF) showing the amount of the survey sample detected by distance downstream from RBR Dam. This simulation used weights for responding to temperature stimuli that were 30% weaker than the weights used to obtain the best simulation.

Figure D.41 Vertical distribution of blueback herring as given by both actual and virtual hydroacoustic surveys. This simulation used weights for responding to dissolved oxygen stimuli that were 30% weaker than the weights used to obtain the best simulation.


Actual Survey
Virtual Survey
No Actual Survey Data Exists
r^2 = 0.82
Depth (m)
0
-2
-4
-6
-8
-10
-12
-14
-16
-18
-20
-22
-24
-26
-28
-30
-32
-34
-36
-38
0
5
10
15
20
25
% of Fish Sample Detected

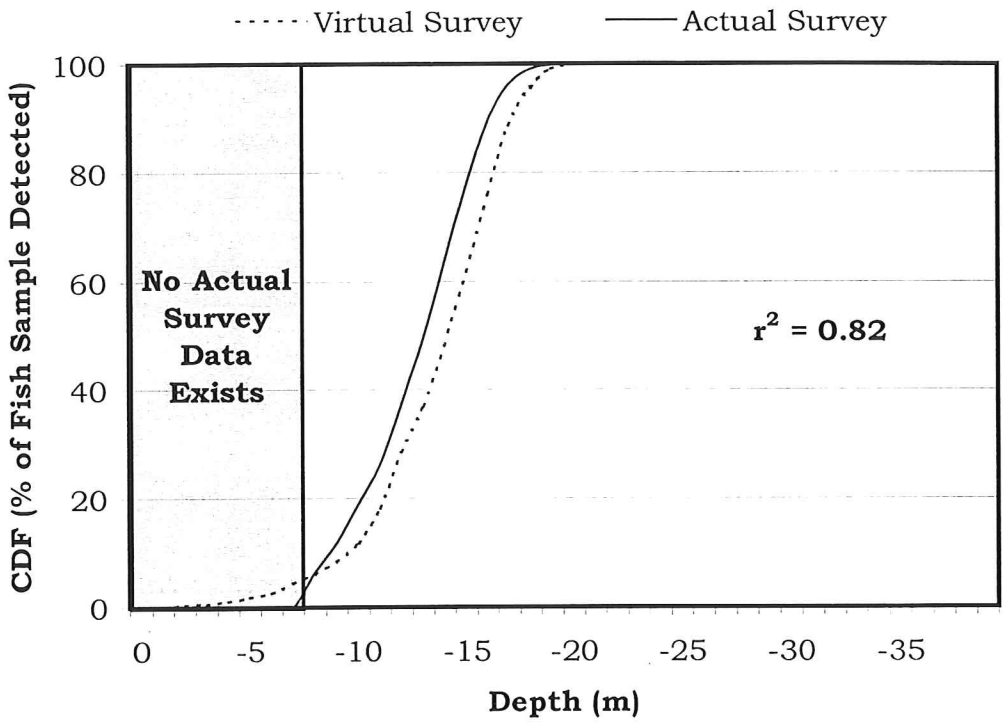


Figure D.42 Cumulative Distribution Function (CDF) showing the amount of the survey sample detected by depth. This simulation used weights for responding to dissolved oxygen stimuli that were 30% weaker than the weights used to obtain the best simulation.

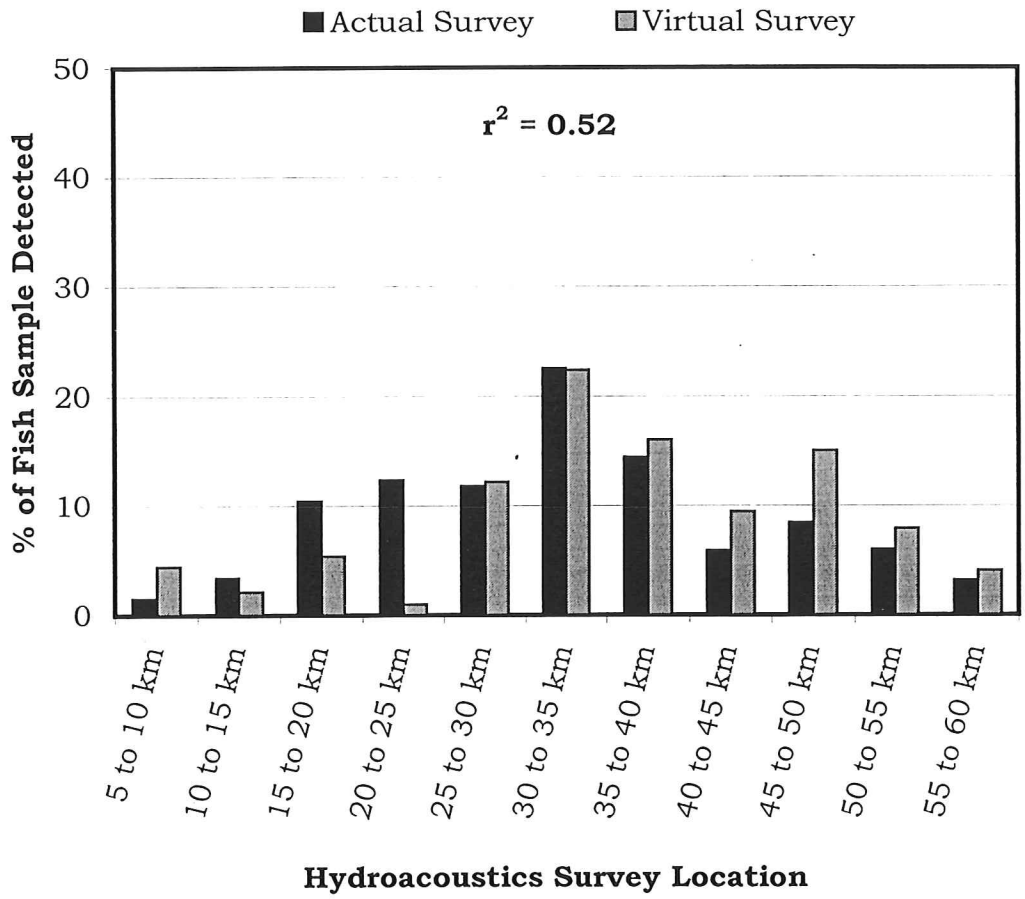


Figure D.43 Longitudinal distribution of blueback herring as given by both actual and virtual hydroacoustic surveys. This simulation used weights for responding to dissolved oxygen stimuli that were 30% weaker than the weights used to obtain the best simulation.

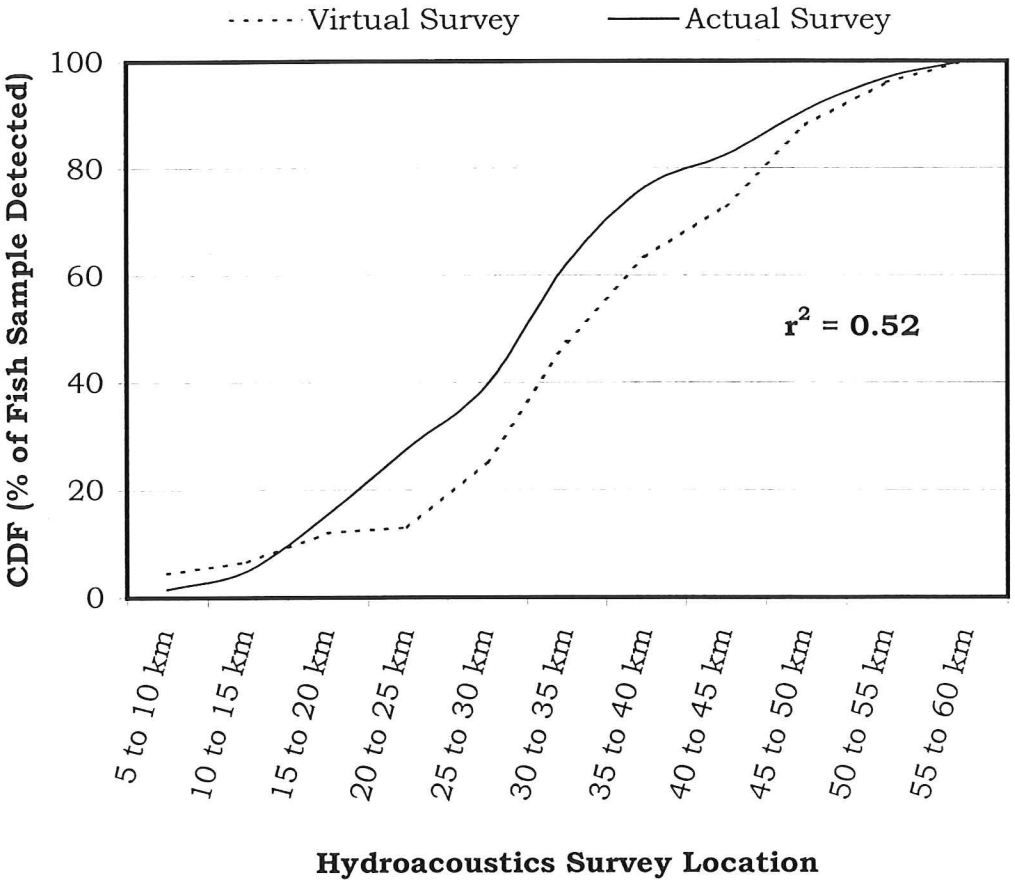
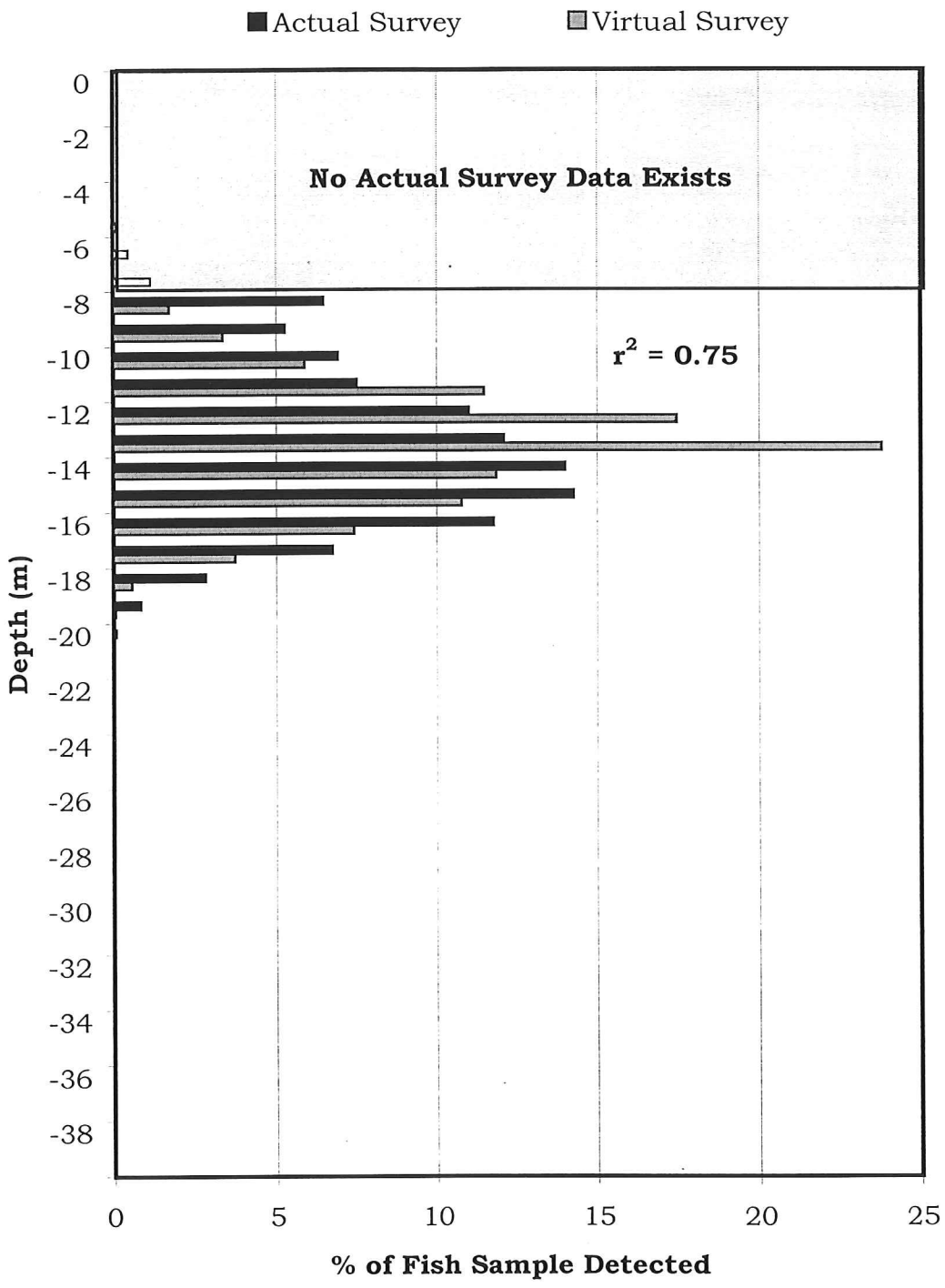


Figure D.44 Cumulative Distribution Function (CDF) showing the amount of the survey sample detected by distance downstream from RBR Dam. This simulation used weights for responding to dissolved oxygen stimuli that were 30% weaker than the weights used to obtain the best simulation.

Figure D.45 Vertical distribution of blueback herring as given by both actual and virtual hydroacoustic surveys. This simulation used weights for randomization (to elicit both longitudinal and vertical volitional swimming) that were 30% weaker than the weights used to obtain the best simulation.


Actual Survey
Virtual Survey
No Actual Survey Data Exists
r^2 = 0.75
Depth (m)
0
-2
-4
-6
-8
-10
-12
-14
-16
-18
-20
-22
-24
-26
-28
-30
-32
-34
-36
-38
0
5
10
15
20
25
% of Fish Sample Detected

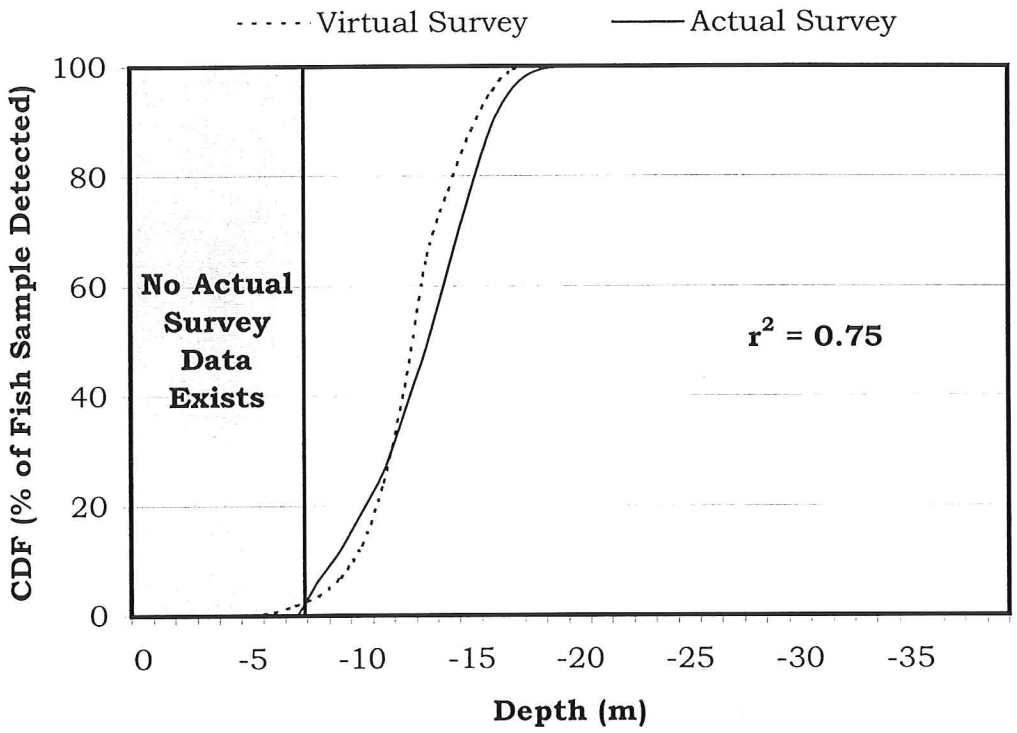


Figure D.46 Cumulative Distribution Function (CDF) showing the amount of the survey sample detected by depth. This simulation used weights for randomization (to elicit both longitudinal and vertical volitional swimming) that were 30% weaker than the weights used to obtain the best simulation.

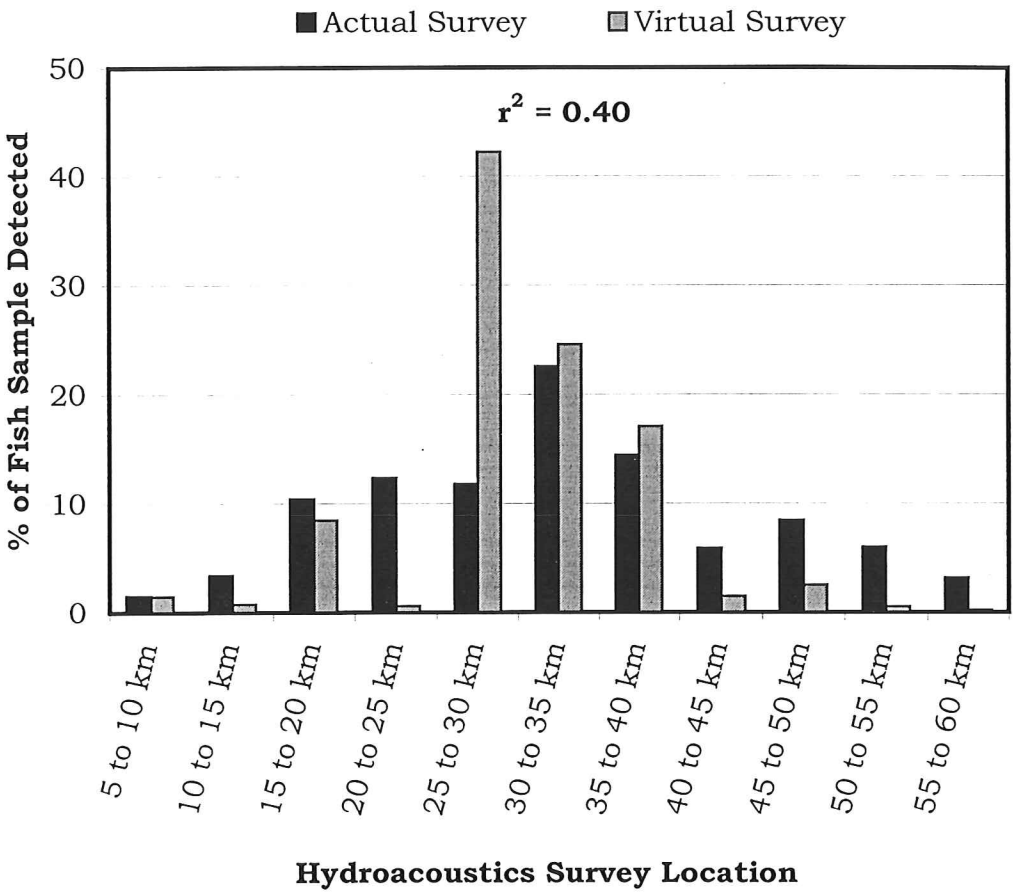


Figure D.47 Longitudinal distribution of blueback herring as given by both actual and virtual hydroacoustic surveys. This simulation used weights for randomization (to elicit both longitudinal and vertical volitional swimming) that were 30% weaker than the weights used to obtain the best simulation.

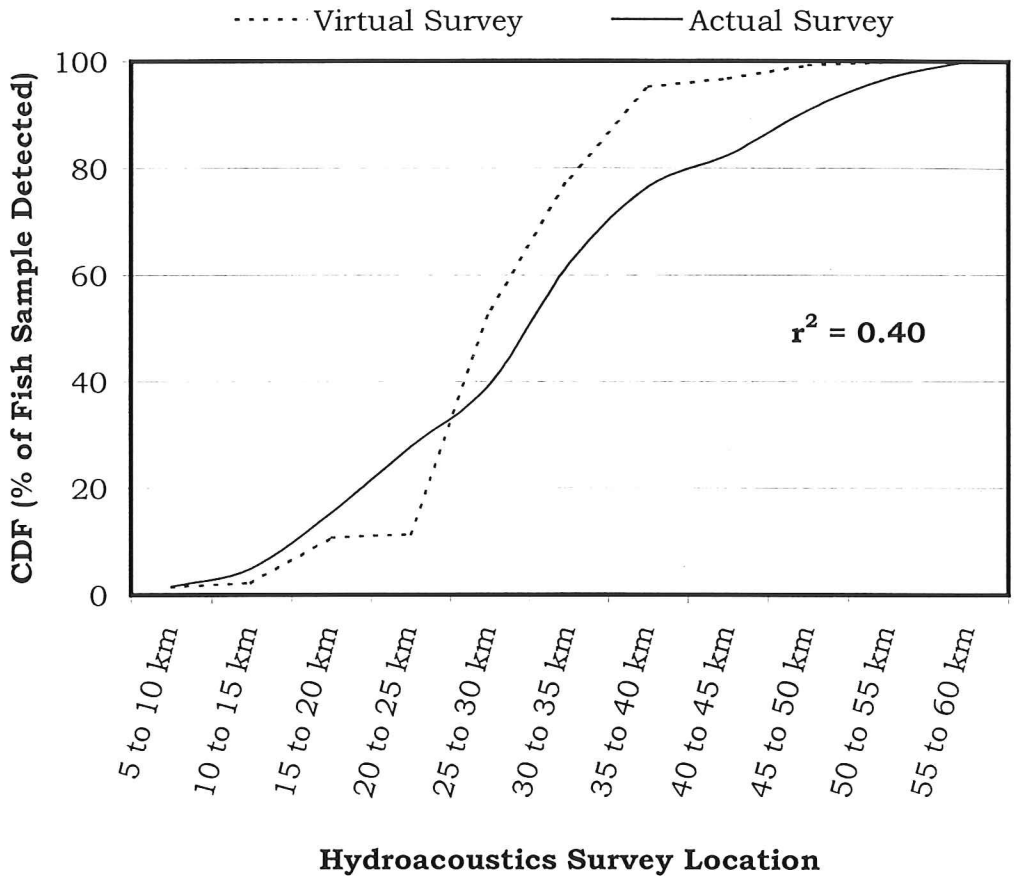


Figure D.48 Cumulative Distribution Function (CDF) showing the amount of the survey sample detected by distance downstream from RBR Dam. This simulation used weights for randomization (to elicit both longitudinal and vertical volitional swimming) that were 30% weaker than the weights used to obtain the best simulation.