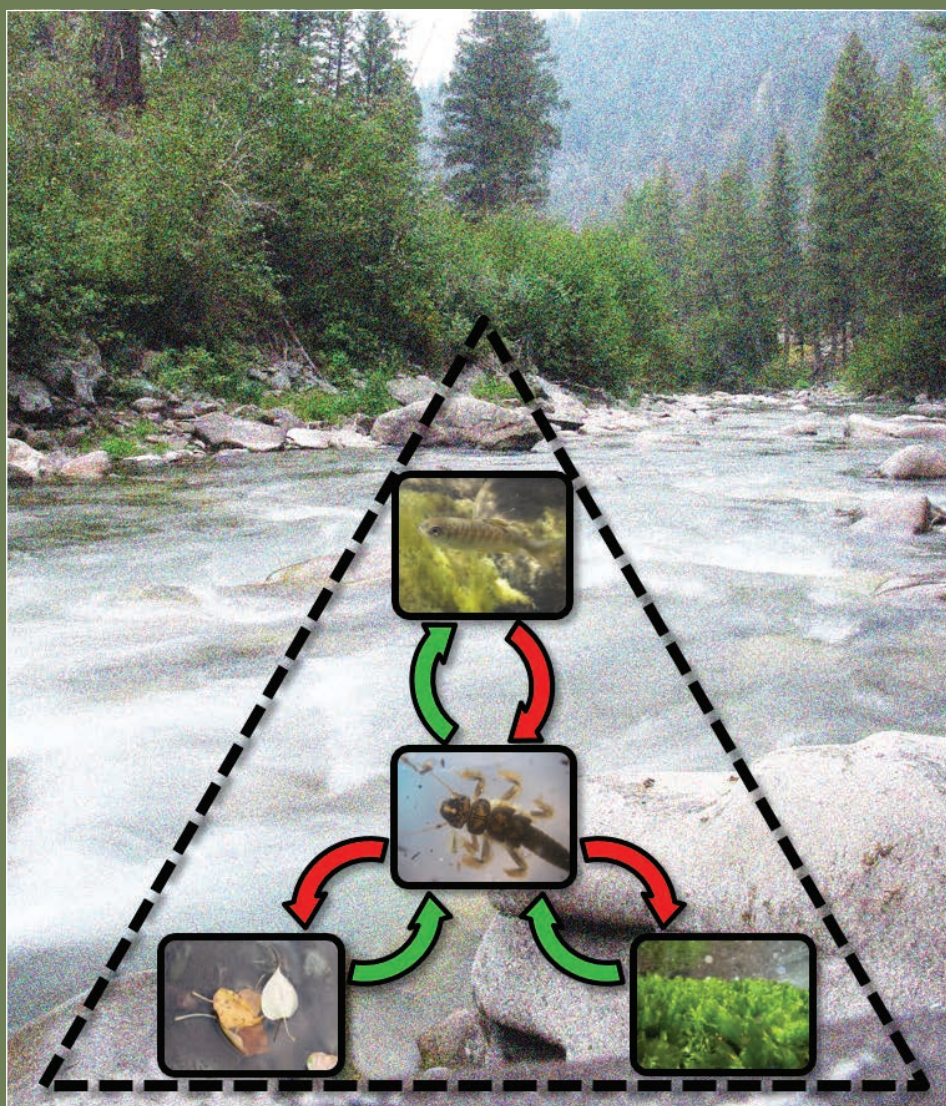


User Manual for the Aquatic Trophic Productivity Model: A River Food Web Simulation Model for Management and Research

Emily J. Whitney, J. Ryan Bellmore, and Joseph R. Benjamin



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Abstract

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The success or failure of fish populations in rivers is intimately linked to a complex and interconnected series of ecological interactions. This complexity can make it difficult to predict how organisms within river ecosystems will respond to management actions and other environmental changes. To aid in solving this dilemma, we constructed a food web simulation model termed the Aquatic Trophic Productivity (ATP) model. The ATP model mechanistically links the success of fish populations to the dynamics of river food webs and the abiotic conditions that influence these webs. This report serves as a user manual for version 3.3 of the ATP model, which was designed to explore how river food webs and fish species, particularly Pacific salmon and trout, respond to management actions and other environmental changes. The report includes a discussion of the model's origins, assumptions, structure, and application. Our primary goal is to provide users the background information needed to apply the model to research and management questions. Specifically, we describe how to parameterize the model and conduct simulations from the model's user interface.

Keywords: River restoration, ecosystem management, Pacific salmon and trout, system dynamics modeling, ecological modeling, decision support tool.

Summary

To understand the success or failure of populations of particular species, we must, among other things, know their energy and material relationships within the ecosystem within which they live (Warren 1971: 290).

This report is a detailed user manual for version 3.3 of the Aquatic Trophic Productivity (ATP) model. This version of the model was designed to allow users to explore how river food webs and fish species, particularly Pacific salmon and trout, respond to management actions and other environmental changes. The primary purpose of this manual is to provide the background information needed by river managers to parameterize the model to local river reaches and explore responses to alternative research and management questions.

The success or failure of fish populations in rivers is intimately linked to a complex and interconnected series of biotic (e.g., predation and competition) and abiotic (e.g., hydrologic and thermal regimes) interactions. This complexity can make it difficult for managers and researchers to envision how organisms that occupy river ecosystems will respond to management actions or other environmental changes. Changes to these ecosystems—whether or not they are made intentionally—will influence the entire ecological network in which these species participate, with effects that can ripple through the food web in complex, nonlinear, and indirect ways (Scheffer et al. 2009, Wootton 1994). Not considering these complexities can result in well-intentioned manipulations that have unintended or even undesirable outcomes (Suding et al. 2004). To aid in solving this dilemma, we constructed a food web simulation model that mechanistically links the success of fish populations to the dynamics of river food webs and the abiotic conditions that influence these webs. Specifically, the ATP model links river food web dynamics to (1) the physical and hydraulic conditions of the stream, (2) the structure and composition of the adjacent riparian zone, and (3) marine-derived nutrients delivered by adult salmon. The model is designed for small to mid-sized rivers where most primary production and secondary invertebrate production occurs in the benthos (rather than in the water column). The model can be used to explore fish and food web responses to a wide range of management actions, from those that represent direct manipulations of the food web (e.g., salmon carcass addition and invasive species), to those that are focused on modifying the physical template upon which these webs of interaction emerge (e.g., habitat manipulations).

- Chapter 1 describes the purpose and intended use of this report and provides a general introduction to the ATP model, including our approach to food web modeling, a general description of the model, and model applications.
- Chapter 2 describes how to use the ATP model, including accessing the model, navigating its interface, data requirements and parameterization, conducting manipulative simulations, and troubleshooting modeling issues.
- Chapter 3 provides step-by-step directions for running model manipulations using a built-in example.
- Chapter 4 details the structure of the ATP model. The model tracks the daily biomass dynamics of different components of a simplified river food web, including juvenile salmon and trout, aquatic and terrestrial invertebrates, periphyton, terrestrial detritus (leaf litter), and salmon carcass and egg biomass (e.g., marine-derived nutrients). This chapter describes how the biomass of each of these food web members, or stocks, is represented in the model and the processes that affect the dynamics of each stock.

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Chapter 1: Introduction to the ATP Model

1.1 What Is the ATP Model?

The Aquatic Trophic Productivity (ATP) model is a mathematical food web model that simulates the capacity of river ecosystems to sustain fish by explicitly linking these fish to the food webs within which they participate. Initially developed by the U.S. Geological Survey to support U.S. Bureau of Reclamation river restoration projects, the model is a simplified version of real river food webs, whereby aquatic organisms—as well as dead organic matter—are compartmentalized into “trophic groups” that share similar predators and prey (fig. 1). In turn, the dynamics of this generalized web—and the success of specific web members—are linked to the

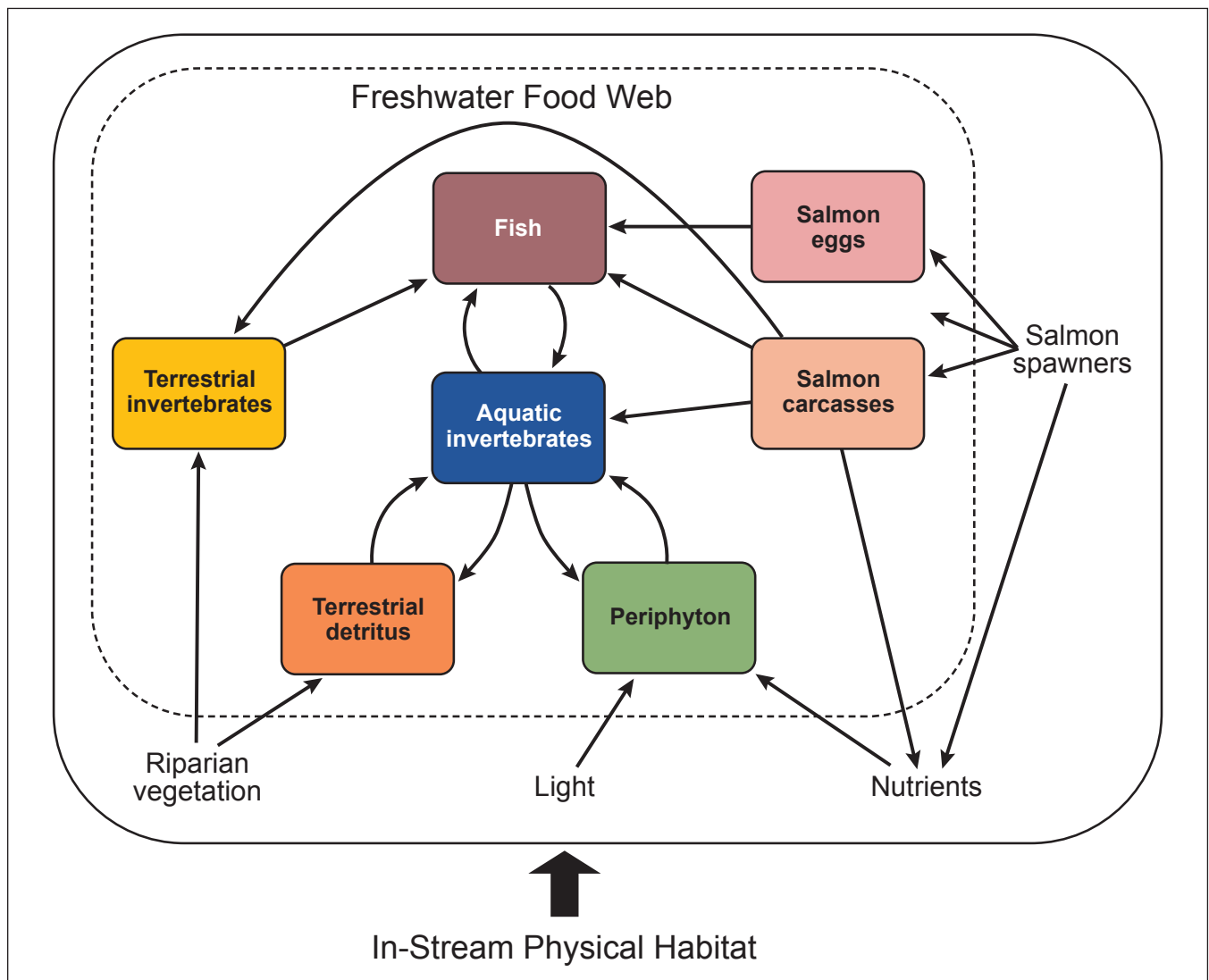


Figure 1—Conceptual diagram of the Aquatic Trophic Productivity model, illustrating (1) biomass stocks of organisms and organic matter (rectangular boxes); (2) consumer-resource interactions that link biomass stocks; (3) inputs of energy, nutrients, and organic matter from outside the system (salmon spawners, light, nutrients, and riparian vegetation); and (4) the reliance of these interactions on instream physical habitat.

physical, chemical, and hydraulic conditions of the river, as well as the structure and composition of adjacent riparian vegetation. The modeling framework assumes that the general dynamics of river food webs can be predicted if the dynamics of these environmental factors are known. Following this assumption, the ATP model can be used to explore how environmental changes wrought by alternative management actions might affect the overall dynamics of the food web and the performance of specific food web members—particularly fish.

This version of the ATP model was coded to explore how the biomass of salmonids (i.e., salmon and trout) in a river reach responds to alternative management actions. However, the model is flexible and can be adjusted to explore a variety of applied and basic research questions.

1.2 Document Purpose

This report serves as a detailed user manual for version 3.3 of the ATP model. Its primary purpose is to provide the background information needed by river managers and other interested parties to parameterize the model to local river reaches and explore responses to alternative research and management questions. The manual accompanies a user-friendly graphical interface to the model that was designed to make it accessible to a wide user group. Users can get started by exploring and running the model through the user interface (<https://exchange.iseesystems.com/public/ryan-bellmore/atp/index.html#page1>). The interface includes background information on the model and basic instructions for conducting model simulations. Users need not be experts in the modeling software, but they should be familiar with, and have data available for, the river site that they intend to model.

This manual provides further details on the structure of the model, how it can be applied, and step-by-step instructions on how to use it. Some of this information has been documented previously (Bellmore et al. 2014, 2017; Benjamin and Bellmore 2016), but is compiled here for reference. The manual is designed to be read in sections as needed. Before applying the ATP model to a new river reach, we recommend that the reader first review chapter 1.

1.3 Why Food Web Modeling?

It has long been appreciated that the success of any particular population is linked to the success of other populations in the ecosystem and the ecological interactions that connect them (Elton 1927, Forbes 1925). Although the targets of management actions are frequently focal species (i.e., those species that have economic or cultural value), management efforts also influence the larger network

in which these species participate, with effects that can ripple through the food web in complex, nonlinear, and indirect ways (Scheffer et al. 2009, Wootton 1994). Not considering these complexities can result in well-intentioned manipulations that have unintended or even undesirable outcomes (Suding et al. 2004). Thus, predicting how species of interest respond to management actions requires holistic approaches that explicitly account for these webs of interactions (Vander Zanden et al. 2006).

River ecosystems are a good example of the need for broader systems approaches to inform management. In rivers, a common management goal is the recovery of threatened or endangered fishes. Assessing potential responses to these actions, however, has traditionally centered on the direct effects of physical habitat on target fish populations (Neil 2001)—a focus driven by a long-standing assumption that physical habitat structure is the primary regulator of fish populations in rivers (Wipfli and Baxter 2010). That said, numerous studies have illustrated that riverine fishes are also strongly influenced by food web interactions, such as food availability (e.g., Kiffney et al. 2014, Richardson 1993); competition for shared food resources (e.g., Bellmore et al. 2013, Davey et al. 2006); and predation by organisms that occupy higher trophic positions (e.g., White and Harvey 2001, Yard et al. 2011). Moreover, many management actions—such as nonnative species removal, hatchery supplementation, and nutrient augmentation (e.g., the addition of salmon carcasses)—are direct food web manipulations that cannot be adequately evaluated with habitat-focused approaches.

Dynamic food web models, even relatively simple ones, can be valuable tools for exploring responses to a wide variety of management alternatives. Although food web models have rarely been applied to rivers (but see McIntire and Colby 1978, Power et al. 1995), they have a long history in the field of ecology (Gotelli 2001, Pimm 2002), and there have been ongoing calls for their incorporation into riverine fisheries management (Naiman et al. 2012). One of the strengths of this approach is that, unlike many statistical and habitat-based fisheries models, dynamic food web models are rooted in—and constrained by—the fundamental laws of thermodynamics (e.g., conservation of energy). The production of a population cannot exceed the availability of that population's prey and the efficiency at which consumed prey is converted into biomass (Lindeman 1942). Moreover, these models can easily be adapted to different environmental contexts by adding or subtracting different species from the food web, and by linking physiological rates of web members (e.g., consumption and respiration rates) to local environmental conditions, such as water temperature and channel hydraulics (Doyle 2006, Power et al. 1995).

1.4 Model Applications

This version of the ATP model was specifically structured to explore responses of stream salmonids (salmon and trout) to alternative management actions and other environmental changes. The general structure of the model, however, is valid in all river ecosystems in which most primary and secondary production occurs on the streambed (rather than in the water column) and where fishes primarily eat invertebrates.

Once the model is parameterized for a specific river reach (or series of river reaches), it can be used to simulate the seasonal biomass dynamics of fish, aquatic invertebrates, periphyton, and terrestrially derived detritus, and how these biomass dynamics change when the user manipulates the environmental conditions of the reach. The model includes a built-in interface designed to allow users to easily manipulate environmental conditions to represent potential changes that might occur with alternative management actions or other environmental alterations (e.g., climate change or shifts in riparian vegetation composition). Although the model has numerous potential applications, below we list six broad management actions and research questions that could be explored via ATP model simulations.

1.4.1 Riparian Management

Changes to riparian vegetation can influence river food webs via multiple pathways. Riparian vegetation structure and composition influence the quantity and quality of terrestrial organic matter inputs to rivers (e.g., leaf litter and terrestrial invertebrates) (Minshall and Ruggenski 2006, Wipfli 1997). Riparian vegetation also shades the stream, modulating water temperatures and controlling the amount of light available for aquatic primary production (Swanson et al. 1982). This model can be used to directly manipulate all these pathways to explore how alternative management actions in the riparian zone, such as logging within riparian zones, riparian vegetation restoration (i.e., tree planting), changes in the riparian community, or natural forest disturbances (e.g., fire, blowdowns, and floods) influence river food webs, and ultimately fish.

1.4.2 Species Introductions

Numerous studies have clearly illustrated that invasive species can significantly alter riverine food webs via a variety of mechanisms, e.g., rerouting basal primary productivity (Hall et al. 2006), modifying nutrient cycling (Covich et al. 1999, Strayer et al. 1999), competing with or preying on desired native organisms (Lepori et al. 2012, Simon and Townsend 2003), and potentially reducing the resilience of the overall community (Olden et al. 2004). Understanding the impacts of invasive species—and if or how they can be controlled—often necessitates a food web

approach. The ATP model can be used to explore responses to species invasions, or alternatively, species extinctions. The current model allows users the opportunity to explore the potential impacts of adding an additional population of fishes that competes with the “target” population of juvenile salmon and trout for food, and also directly preys upon these target fish. This “non-target” stock does not necessarily represent any specific nonnative species, but rather represents the broader community of native and nonnative fishes with which juvenile salmon and trout frequently interact. This feature was included to allow users to explore how changing the structure of the food web might influence responses to alternative management activities (see Bellmore et al. 2017) (for model details, see section 2.4.2, “Food Web Manipulations”). However, advanced users could also code specific nonnative or invasive species into the food web to explore a wide range of questions. For example, Bellmore and others (2017) used the ATP model to evaluate food web responses to invasive New Zealand mudsnails (*Potamopyrgus antipodarum*), and Daniels and others (2018) used the model to explore how changes in aquatic invertebrate species richness influence freshwater salmon production.

1.4.3 Nutrient Augmentation

Nutrient augmentation represents the purposeful addition of nutrients or organic matter to streams to stimulate biological productivity. In the Pacific Northwest of the United States, for example, adult salmon carcasses (or a similar “analog” material) are frequently added to rivers in an attempt to promote juvenile salmon growth and survival by increasing available food resources (Collins et al. 2016, Kohler et al. 2012). In other river systems, dissolved nutrients (such as phosphorus) are directly added to streams to stimulate basal primary production (Hoyle et al. 2014). The ATP model can be used to evaluate how these nutrient additions influence the dynamics of the food web and capacity of the system to support fish (Bellmore et al. 2017, Benjamin and Bellmore 2016). In particular, the model includes multiple pathways by which adult salmon or marine-derived nutrients influence aquatic food webs (i.e., from bottom-up nutrient pathways to direct consumption of carcasses and eggs by aquatic invertebrates and fish).

1.4.4 Physical Habitat Restoration

The focus of many river restoration actions is the manipulation of physical habitat features within the stream or the adjacent floodplain, such as the addition of large woody debris or reconnection of floodplain side channels. Although these projects do not represent direct manipulations of the food web, they do modify

the physical template, which can indirectly influence food webs via multiple pathways. For instance, the morphology of rivers influences hydraulic conditions such as channel width, water depth, velocity, and shear stress. In turn, these hydraulic conditions influence the amount of light reaching the streambed to fuel photosynthesis, the amount of wetted area for biological productivity to occur, the capacity of the river reach to retain organic matter and organisms, and the amount of habitat that is suitable for fish. The ATP model incorporates all these linkages, and thus can be used to evaluate how changes in channel morphology (or hydrology) influence food web dynamics (Bellmore et al. 2017, Benjamin and Bellmore 2016, Benjamin et al. 2018).

1.4.5 Climate Change

Climate change may significantly alter stream temperatures and flow regimes, as well as the adjacent terrestrial ecosystem (Carpenter and Fisher 1992). These changes will affect all freshwater organisms, and thus the associated dynamics of aquatic food webs. The ATP model can be used to explore how climate change-induced shifts in water temperature, flow regime, and riparian vegetation influence aquatic food web dynamics. These simulations can also be combined with the management actions listed above to explore how future climate conditions will mediate (or potentially negate) desired responses to management.

1.4.6 Limiting Factors Analysis

In addition to the management actions described above, the ATP model can also be used to explore and rank the environmental factors that limit biological productivity. By manipulating the inputs to the model, users can test the “sensitivity” of model results to different environmental conditions. For example, users can adjust nutrient concentrations, water temperatures, discharge, stream shading, and leaf litter to see how fish populations respond to changes in each condition individually or in combination. We strongly encourage all users to conduct these informal sensitivity analyses prior to conducting more structured analyses. Informally gaming the model in this way helps users understand the dynamics of the model, as well as identify potential errors in model parameterization. Moreover, these analyses can be used to identify the types of manipulations that are most likely to achieve desired outcomes (e.g., increased fish biomass).

1.5 Model Description and Approach

1.5.1 Stella Software and System Dynamics Modeling

The ATP model was developed using Stella Architect™ modeling software (ISEE Systems, Lebanon, New Hampshire, <https://www.iseesystems.com>).¹ Stella Architect is an icon-based model building and simulation software application designed for “system dynamics” modeling, which is a structured approach for understanding the nonlinear behavior of complex systems (such as ecosystems) over time. The structural elements of system dynamics models include stocks, flows, and converters. Stocks are measurable quantities such as the number of individuals in a population, or, in the case of the ATP model, the biomass of trophic groups such as fishes, aquatic invertebrates, or periphyton. Flows are processes that change the quantity—positively or negatively—of a stock over time. In the ATP model, this includes processes that increase the biomass of a stock such as periphyton production and food consumption, and processes that decrease the biomass of stocks such as predation and mortality. Converters are components that affect the rate of change (e.g., consumption and mortality rates) and are connected to flows and other converters via “connectors.” Once constructed, system dynamics models generally contain numerous feedback loops, whereby the size of stocks feeds back to influence the magnitude of flows. For example, as the biomass of consumers increases, so does the consumption of their prey (e.g., periphyton). This reduces the amount of prey available for consumption, thus the biomass of the consumer decreases. An example of a simple Stella system dynamics model that includes all these components is shown in figure 2.

We chose to develop the ATP model using Stella because it allows users to visualize the structure of the model—i.e., the feedbacks and linkages—that determine model behavior. Given the complexity of the model, we deemed this transparency to be necessary. Moreover, Stella allows for the construction of user-friendly interface pages (also known as model graphical user interfaces [GUIs]) (hereafter referred to as “Interface”), allowing individuals with no modeling experience to access the model.

¹ The use of trade or firm names in this publication is for reader information and does not imply endorsement by the U.S. Department of Agriculture of any product or service.

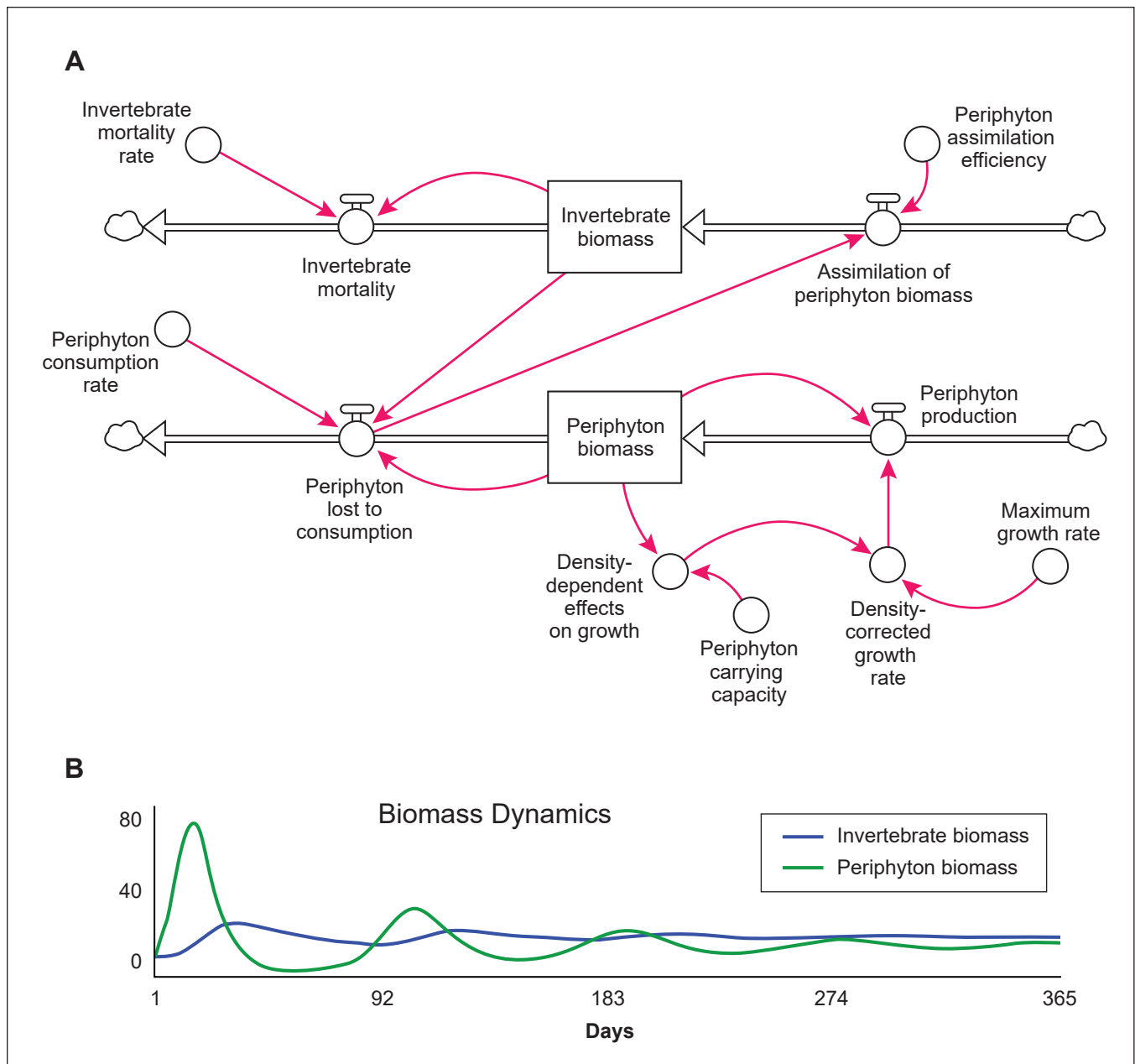


Figure 2—Example of system dynamics model developed in Stella Architect: (A) A simplification of the predator-prey linkages incorporated into the ATP model. The rectangular boxes are the “stocks,” which track aquatic invertebrate and periphyton biomass; the large arrows are the “flows” that represent gains and losses of biomass; and the circles are “converters” that determine the size of inflows and outflows. The narrow red lines are “connectors” that represent linkages between different model components. (B) In this model, biomass dynamics for aquatic invertebrates and periphyton oscillate over time. These oscillations dampen as new equilibrium values are reached (i.e., as the inflows for each stock are balanced by the outflows).

1.5.2 General Model Structure

The model contains seven biomass stocks (i.e., state variables): (1) target fish, (2) aquatic invertebrates, (3) terrestrial invertebrates, (4) instream primary producers (periphyton), (5) terrestrial detritus (leaf litter), (6) salmon eggs, and (7) salmon carcasses (fig. 1). In the model, aquatic invertebrates consume periphyton, terrestrial detritus, and salmon carcass material, while fishes consume aquatic and terrestrial invertebrates as well as salmon eggs and carcasses. Depending on model settings, a stock of non-target fish can also be added to the modeled food web that both competes with the target fish stock for food and directly preys upon the target fish. This stock is meant to represent the community of native and nonnative fishes with which juvenile salmon and trout frequently interact. In the Pacific Northwest, for example, this might include native species such as sculpin (*Cottus* spp.), mountain whitefish (*Prosopium williamsoni*), and adult bull trout (*Salvelinus confluentus*), as well as nonnative species such as smallmouth bass (*Micropterus dolomieu*) and brook trout (*S. fontinalis*).

As in all ecosystems, the modeled food web is an open system, in that energy and materials enter the system from external locations. These external inputs represent the raw ingredients that fuel aquatic productivity, and include (1) light and nutrients, which provide energy and materials needed for periphyton production; (2) lateral inputs from the riparian zone, which provide terrestrial detritus (leaf litter) and direct food resources for fish (terrestrial invertebrates); and (3) returning adult salmon, which represent a source of marine carbon and nutrients (“marine-derived nutrients”) that are incorporated into the food web via nutrient uptake by periphyton and direct consumption of carcass material by fish and invertebrates (see chapter 4).

Finally, the physical conditions of the stream and the adjacent riparian zone determine the dynamics of the modeled food web. **Water temperature** controls the bioenergetics of organisms (production, consumption, and respiration rates) and decay rates of organic matter. **Channel discharge and hydraulics** directly influence channel width, water depth, velocity, and shear stress, which in turn influence the amount of light reaching the streambed to fuel photosynthesis, the amount of wetted area available for biological productivity to occur, the capacity of the river reach to retain organic matter and organisms, and the amount of habitat that is suitable for fish. **Incoming light and shading** also determines how much photosynthetically active radiation is available to support periphyton production. **Water turbidity**, in conjunction with water depth, determines how much of this light is attenuated before it reaches the streambed. The type and cover of **riparian vegetation** influences the flux of terrestrial leaf litter and invertebrates to the stream and the proportion of the stream that is shaded. The details of all these mechanistic linkages can be found in section 4.2, “Inflows and Outflows.”

1.5.3 Spatial and Temporal Scales

The ATP model can be used to simulate the biomass dynamics of food web members across a range of temporal and spatial scales. Biomass estimates are produced on a daily time step, but these daily estimates can be summarized at different temporal scales, such as seasonally or annually. The advantage of daily estimates is that potential bottlenecks or temporal limitations to each trophic group can be identified, as well as the associated underlying mechanisms responsible for these limitations. From a spatial perspective, the model was designed for exploring food web responses at the scale of river reaches or geomorphic segments (hundreds of meters to tens of kilometers). Although the model **can** be parameterized for larger or smaller river lengths, given that habitat conditions are averaged within the modeled reach, it may not make ecological sense to model areas that are much smaller (e.g., channel units) or substantially larger (e.g., entire watersheds). However, advanced users could link multiple river reaches end-to-end—via downstream transport of organic matter (periphyton, terrestrial detritus, and invertebrates) and bidirectional movement of fishes—to simulate responses for larger spatial domains, such as whole watersheds. This type of network-scale view of food webs may result in emergent dynamics that could greatly contribute to the understanding (McCluney et al. 2014, Polis et al. 2004) of how local management efforts interact to influence watershed-scale processes.

1.5.4 Fundamental Assumptions

Like many ecological models, the ATP model is based on numerous assumptions. For instance, each equation and associated parameter value is an assumption about how a given aspect of the river food web operates. Listed below are fundamental model assumptions of which all users should be aware.

1. Implicit within the structure of the model is the assumption that the general dynamics of river food webs can be estimated when organisms are compartmentalized into trophic groups. This is a critical assumption because the structure of the modeled food web is much simpler than real river food webs (Bellmore et al. 2013, Cross et al. 2011). However, incorporating more complexity may not make the model more predictive or useful (Ford 2010). For example, complex food web models often produce results that are extremely difficult to interpret, introduce numerous parameters of unknown value, and frequently exhibit behavior that is chaotic or unstable; all these things serve as justification for a more simplified approach.
2. Most of the primary and secondary production that fuels the food web occurs in the benthos (rather than in the water column). In general, this

assumption is valid for streams and small to mid-sized rivers (Allan and Castillo 2007), for which the ATP model is best suited. The model is not valid in larger rivers, where a significant portion of primary and secondary production is represented by pelagic phytoplankton and zooplankton.

3. Fish are primarily insectivores (i.e., they do not eat detritus or algae), or in the case of the non-target fish stock, both insectivores and piscivores. This assumption is valid for many freshwater salmonids (Bellmore et al. 2013, Rader 1997, Waters 1969), particularly juvenile salmon and trout. Advanced model users, however, can alleviate this assumption by modifying the trophic relationships within the model (e.g., allow fish to consume periphyton).
4. River food web dynamics can be modeled if certain conditions of the physical (e.g., temperature, discharge, channel morphology, and hydrology) and riparian (structure and composition of riparian vegetation) environment are known. With this assumption, the ATP model can be used to explore relative changes in the direction and magnitude of biomass for each trophic group following restoration or management actions that alter these environmental conditions.

1.6 How the ATP Model Runs

The model runs on a daily time step and tracks biomass of food web members through time, specifically the biomass of periphyton, terrestrial detritus, aquatic invertebrates, and juvenile fish in grams of ash-free dry mass (AFDM). We chose to use AFDM because it eliminates the variability resulting from water content and allows comparisons among trophic levels. This biomass measure does not indicate the number of organisms nor their size or length. Graphs on the Interface show both the total biomass of food web members for the modeled reach and the per-square-meter estimates. Figure 3 shows an example output from the ATP model that illustrates these biomass dynamics.

During each model run, the ATP model simulates 10 years (3,650 days, starting January 1) of biomass dynamics for each of the stocks in the model (see chapter 3, “Built-In Model Example,” for details on these biomass dynamics). The environmental conditions used to parameterize the model are repeated each year. For example, water temperature and flow regimes are held exactly the same from one year to the next. The 10-year model run allows the model time to “burn-in” to these initial conditions, i.e., for modeled biomass dynamics to reach equilibrium with the environmental conditions provided by the user. The outputs shown on the model Interface display the final year (days 3,285 to 3,650) of this 10-year simulation, after equilibrium has been reached (fig. 4). There may be instances in which equilibrium

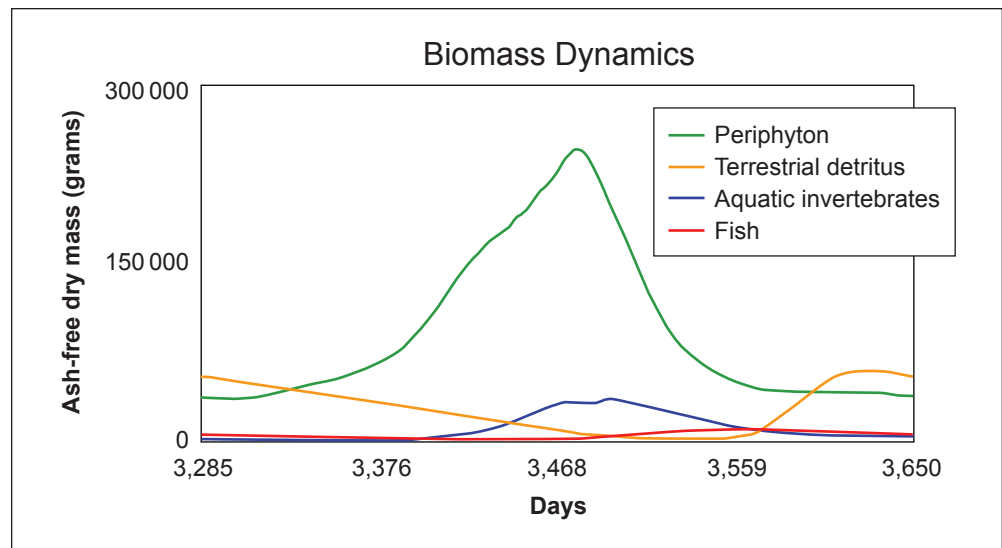


Figure 3—Example of biomass dynamics produced by the Aquatic Trophic Productivity model. This graph shows the daily biomasses in grams of ash-free dry mass for the last year of a 10-year model simulation. Biomasses oscillate over time owing to a combination of seasonally changing environmental conditions, such as water temperature and discharge, and internal predator-prey interactions.

is not reached by the final year of the simulation (see section 2.5, “Troubleshooting”). This version of the ATP model is deterministic (versus stochastic). Thus, running the model multiple times will produce the exact same output if no changes are calculated).

Although model results are shown only for a single reach of interest, the model also includes an “upstream” reach (represented in an array). This upstream reach is parameterized with the same environmental parameters as the “modeled” reach and serves as an upstream boundary condition (assuming that environmental conditions are relatively similar for a given distance upstream). The upstream reach exports organic matter and organisms to the modeled reach of interest (see section 4.2.7, “Upstream Inputs”). Having this upstream reach allows users to hold upstream conditions constant as the modeled river reach is manipulated via alternative treatment experiments. In other words, when the model is manipulated on the Interface, these changes influence only the downstream modeled reach. Upstream conditions remain unchanged, and thus upstream inputs of organic matter and organisms remain unchanged. Though not implemented here, this domain structure provides the framework for linking multiple reaches together in a spatially explicit manner (see section 1.5.3, “Spatial and Temporal Scales”).

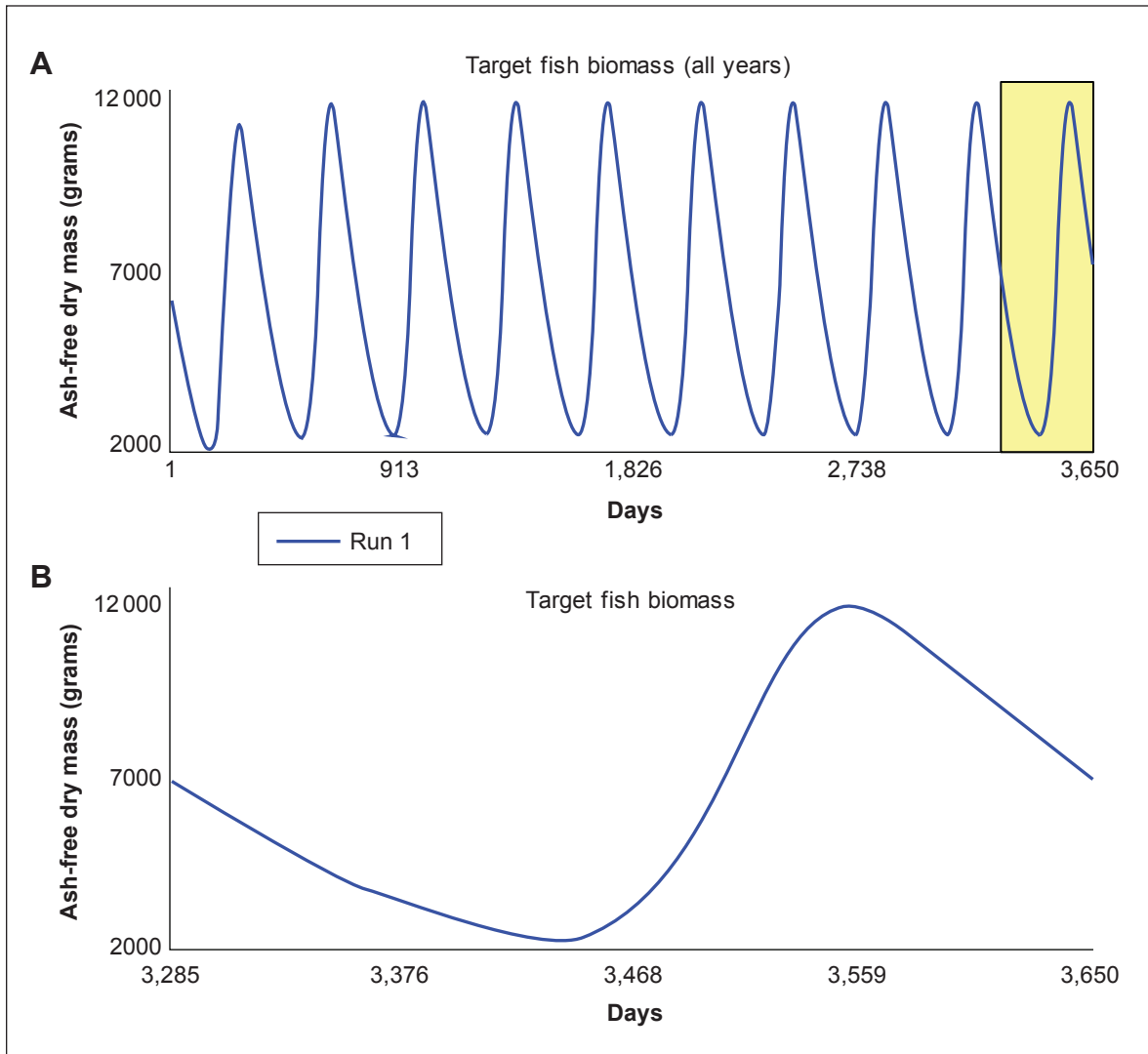


Figure 4—Biomass dynamics of target fish: (A) All 10 years (3,650 days) of biomass dynamics. In this example, target fish biomass levels equilibrate within 3 years (~1,000 days), and the same annual pattern is repeated thereafter. (B) The final year of the simulation (yellow box in diagram A) is expanded in this figure and on the target fish biomass graph on the Interface to highlight the seasonal biomass dynamics.

1.7 Interpretation of Model Simulations

The ATP model was designed to explore how river food webs and associated fish populations respond to alternative management actions. Thus, model users may ask—and rightly so—are ATP model predictions valid? This is an important question that frequently reveals considerable confusion about the meaning of having a “valid” model (Rykiel 1996). The ATP model is “conceptually valid” in that the theories and assumptions underlying the model are justifiable. All the mathematical relationships in the model are based on scientific evidence (although some relationships have more scientific support than others). The ATP model has also been shown to be “operationally valid.” That is, the predictions of the model, in terms of the simulated biomasses of different food web members, are similar to those that have been measured in the field (see Bellmore et al. 2017). However, this does not mean that model simulations should be interpreted as truth. Rather, ATP model simulations should be thought of as testable hypotheses about what **might** happen under alternative future conditions. These **hypotheses** can provide the basis for decisionmaking within the context of an adaptive management plan (Walters 1986). Although results from the model may prove to be wrong, information collected by subsequent monitoring can be used to refine model parameters, the structure of the model, and even the underlying knowledge and assumptions on which the model is based (Power 2001).

ATP model simulations can also be used to explore how and why given responses may (or may not) occur. Users can apply the ATP model to trace the causal pathways by which management actions or other environmental changes might influence river food webs, and ultimately the capacity for river ecosystems to sustain fish production. Using the model to explore the mechanisms underlying the ecosystem response to management actions in this way can improve decisionmaking by fostering a deeper understanding of system connectedness and dynamics.

Use of the ATP model is more appropriate for comparing **relative** differences among alternative scenarios than it is at predicting the **absolute** value (e.g., fish biomass) for a given scenario. The exact biomass values produced by a given scenario can be highly sensitive to the value of model parameters, many of which are highly uncertain. However, relative differences among numerous model scenarios are likely to be robust to this parameter uncertainty. For example, if the model predicts that scenario Z has greater fish biomass than scenario Y, and scenario Y has a greater biomass than scenario X, this ranking is likely to be insensitive to changing the values of uncertain model parameters. We therefore encourage the use of the ATP model as a tool to explore **relative** changes in the biomass of fish and other food web members. Less focus should be given to the absolute biomass values

produced by the model than the relative differences. However, users should check that modeled biomass values are within the range that might be expected for the modeled river reach. To check this, users may find it helpful to compare modeled values to those from empirical studies from nearby streams and watersheds. For periphyton and aquatic invertebrates, modeled values are reported in units similar to those reported in empirical studies (grams of AFDM per square meter). For fish, users may find it useful to convert AFDM to wet mass or convert from mass to number of individuals. For salmonids specifically, a conversion factor of 0.2 grams AFDM per 1.0 grams wet mass may be used (Elliott 1976). Users can then convert from wet mass to number of individuals by dividing the wet mass by the assumed size of the average individual (e.g., 10 grams of wet mass equals 10 individual fish if average fish mass is 1 gram).

1.8 Terminology

We use the following modeling terminology throughout this document and on the model Interface:

Term	Definition
Background conditions	Background conditions represent the current environmental conditions of the modeled reach prior to any manipulations .
Environmental conditions	The instream physical habitat and riparian conditions of a river reach (e.g., discharge, water temperature, nutrient concentrations, riparian vegetation cover, etc.).
Environmental parameter	An environmental condition that the user inputs into the model to parameterize the model for a given scenario .
Flow (inflow/outflow)	Flows are processes that change the quantity, positively or negatively, of a stock over time.
Manipulation	Changes to one or more of the environmental parameters of the model. Users may conduct manipulations to explore responses to alternative management actions, or simply to conduct exploratory sensitivity analyses.
Model parameter	A variable used in model equations that defines the relationship between different components of the model. The ATP model is already parameterized with values for all model parameters, which were derived from published literature sources and model calibration (see Bellmore et al. 2017).
Model sensitivity	The response of model outputs to manipulations in environmental parameters or model parameters . “High sensitivity” reflects parameter manipulations that result in relatively large changes in model outputs.
Reach	A user-specified length of river that is being represented by model simulations .
Scenario	A complete set of environmental parameters in the ATP model. Effects of management alternatives or other manipulations are generally assessed by comparing several different scenarios (e.g., background condition scenario versus different manipulated scenarios).
Simulation/simulate	The output of model runs, or act of running the model.
Stock	In the ATP model, stocks track the biomass of different trophic groups (e.g., the mass of periphyton) through time.

Chapter 2: Using the ATP Model

This chapter outlines how to use the Aquatic Trophic Productivity (ATP) model, including accessing the model (section 2.1), navigating the model Interface (section 2.2), data requirements and parameterization (section 2.3), conducting manipulative simulations (section 2.4), and troubleshooting modeling issues (section 2.5).

2.1 Model Access and Compatibility

The ATP model and associated Interface were designed using Stella Architect version 1.6 (ISEE Systems, Lebanon, New Hampshire, <http://www.iseesystems.com>). The model file is compatible with earlier versions of Stella Architect but is incompatible with Stella 10 (and other earlier versions). Users have four options to view and interact with the ATP model (table 1).

1. ISEE Exchange: The model can be run on the ISEE Exchange online modeling platform (<https://exchange.iseesystems.com>) with no software purchase required (search by keyword “ATP”). Model runtime and appearance may differ with Internet browsers. At the time of publication, Google Chrome™ provided the best viewing and fastest run times.
2. ISEE Runtime: The ISEE Runtime software can be purchased from ISEE Systems and allows users to run the model. Moreover, ISEE Runtime will give users the option to save model parameters.
3. ISEE Player: The ISEE Player is a free program that can be downloaded from ISEE Systems and allows users to view the full stock and flow structure of the ATP model, but does not provide access to the Interface page or allow for editing the model structure.
4. Stella Architect: This is ISEE Systems’ flagship software package. In addition to viewing and running the ATP model, Stella Architect allows users to edit the structure of both the model and the Interface but requires purchasing a software license. Note: as this report went to press, a free 1-month trial version of Stella Architect was available for download from ISEE Systems.

Table 1—Software options for using the Aquatic Trophic Productivity model

Product	Run model from interface	View model structure	Edit model structure	Import/export data using Excel™	Save model changes
ISEE Exchange™	✓			✓	
ISEE Runtime™	✓			✓	✓
ISEE Player™		✓			
Stella Architect™	✓	✓	✓	✓	✓

The choice of software depends on the model application. Users who wish to modify the underlying structure of the model or interface need to purchase a Stella Architect license. For most users, we recommend running the model online using the ISEE Exchange. The online platform is free and allows users to run the ATP model on almost any device that is connected to the Internet (including smartphones). The online platform is also a useful tool for educational purposes; i.e., users can learn about river food web dynamics by manipulating different parameters and tracking model behavior. Users can also purchase ISEE Runtime. It is a less expensive software package than Stella Architect, and it allows users to parameterize and run the model from their desktop.

2.2 Navigating the Model Interface

Users can view the structure and explore the behavior of the ATP model from the Interface. The Interface contains five navigation tabs: **Introduction**, **Model Exploration**, **Simulation**, **Citations**, and **Contacts**. The **Introduction** tab provides a brief overview of the ATP model. The **Model Exploration** tab walks the user through the structure of the model and provides general descriptions of the flows that affect model dynamics (see sections 4.1, “Stock Summaries,” and 4.2, “Inflows and Outflows,” for details). From the **Simulation** tab, the user can run the model, adjust parameters to explore different model manipulations of environmental conditions (see section 2.4, “Model Manipulations,” for examples), and view model outputs. The **Citations** tab provides links to papers documenting the model structure and application, and the **Contacts** tab provides contact information for the model designers.

The following section describes the widgets (buttons, graphical and numeric inputs, switches, and graphs) used in the ATP model Interface and includes directions on their use. There is also a “Tutorial” button located on the **Simulation** tab of the Interface that links to this information.

Buttons: Click on buttons to complete specified actions, such as running the model or opening a different page within a navigation tab.

- **Model Control buttons:** These buttons are used for conducting basic model actions, such as running the model and resetting model devices (fig. 5).
Note: buttons will appear grayed out when the model is running or another action is being undertaken.
- **Run:** This completes one model run, simulating 3,650 days (10 years) of biomass stock dynamics.

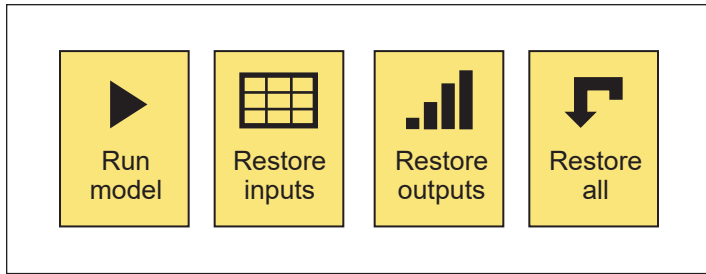


Figure 5—Image of model control buttons.

- **Restore inputs:** This resets all input devices (graphical functions, numeric inputs, etc.) to their original values. This applies to all input devices on every page of the Interface. To restore a single input device to its original value, click on the return arrow that appears next to modified inputs (↶) or use the “Restore” button found on graphical functions.
- **Restore outputs:** This resets the output devices (graphs) and clears model runs. Applies to all output devices on every page of the Interface.
- **Restore all:** This resets all input and output devices to built-in model example values. **No changes are saved.**
- **Annotation buttons:** These buttons open a text box with further information. Click on parameter names listed in italics to open a text box that describes/defines the metric (fig. 6). When done reading, click outside the box to close the annotation box.

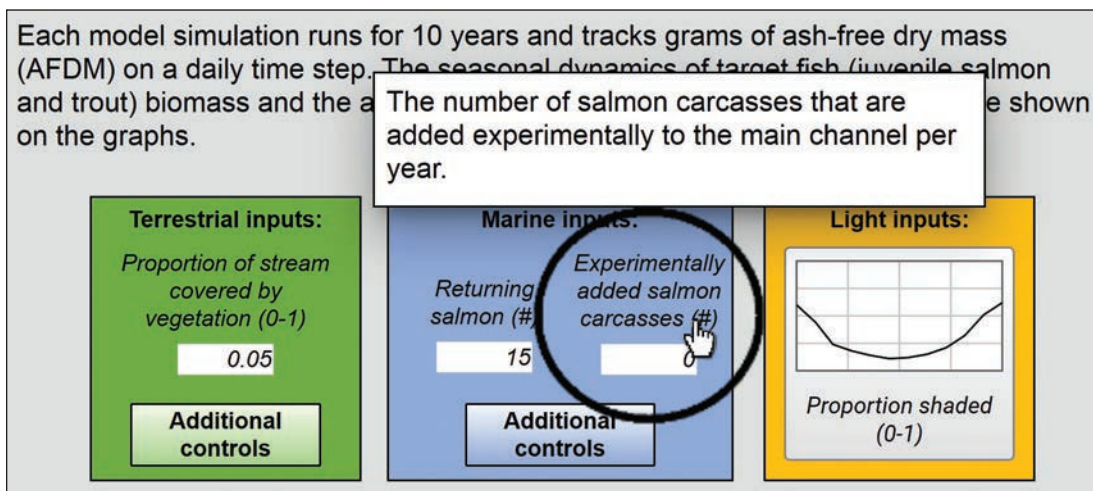


Figure 6—Example of an annotation button.

Graphical functions: Graphical functions are input devices used for parameterizing the model with environmental conditions that are seasonally variable, such as discharge and water temperature (fig. 7). To use a graphical function, click the graph portion of the icon to edit the data points. Trace a new line in the graph window or enter X and Y values by clicking on “Table” in the upper right-hand corner of the graph window.

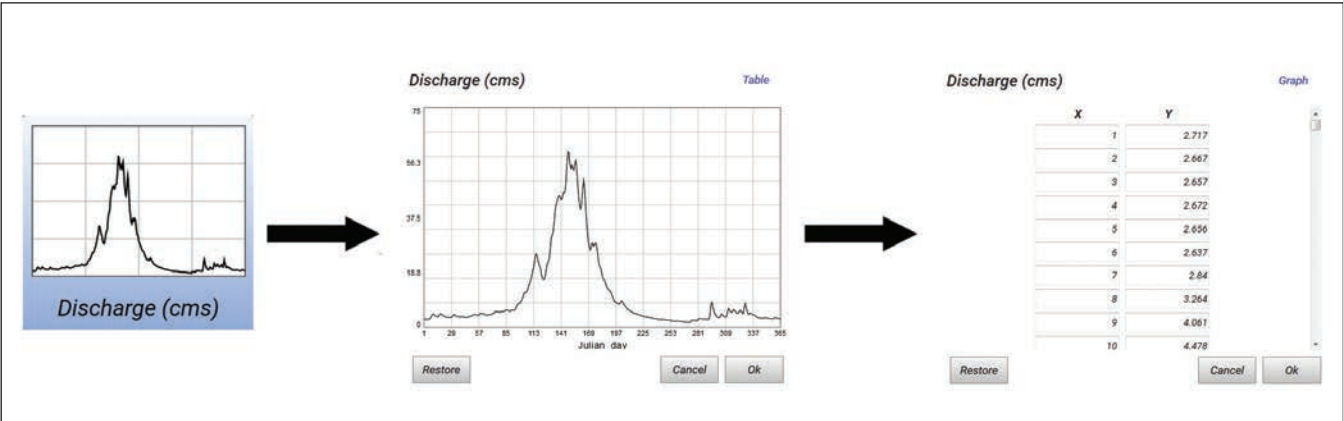


Figure 7—Example of a graphical input.

Numeric inputs: Numeric inputs allow users to adjust the value of constant environment parameters (fig. 8), such as channel slope or the number of returning salmon. To alter values, type a number in the box and then click outside the box to save changes. If the new value is outside the allowable input range (shown in parentheses after the units), the numeric input will reset to the maximum or minimum allowable value, whichever is closer. For example, if a value of 100 is entered for a parameter with an input range of 0 to 1, the parameter value will be set to 1.

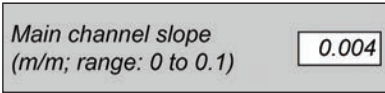


Figure 8—Example of a numeric input.

Switches: Switches turn model components on and off (fig. 9), such as determining the presence or absence of a side channel.

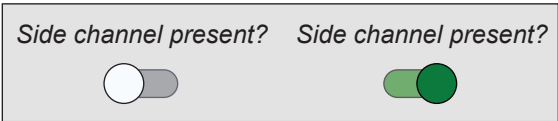


Figure 9—Example of input switch, illustrating the OFF position in gray (left), and the ON position in green (right).

Graphs: Graphs visually display the results of model simulations. Trace or click along the line or bar to display the values at specific time steps (fig. 10). The simulation time step (days modeled since the beginning of the simulation) is shown in the lower right-hand corner of line graphs and along the top of the bars in bar graphs. Graphs present simulation results for the last year of the model run (unless otherwise noted). Line graphs display daily values over 1 year, and bar graphs display the annual average value for the variable. The months of the final year (labeled with the first letter of the month's name) of the simulation are shown along the X-axis of the line graphs.

For information on how to use Stella Architect or other ISEE Systems products, see the online documentation at <https://www.iseesystems.com/resources/help/v1-6/default.htm>.

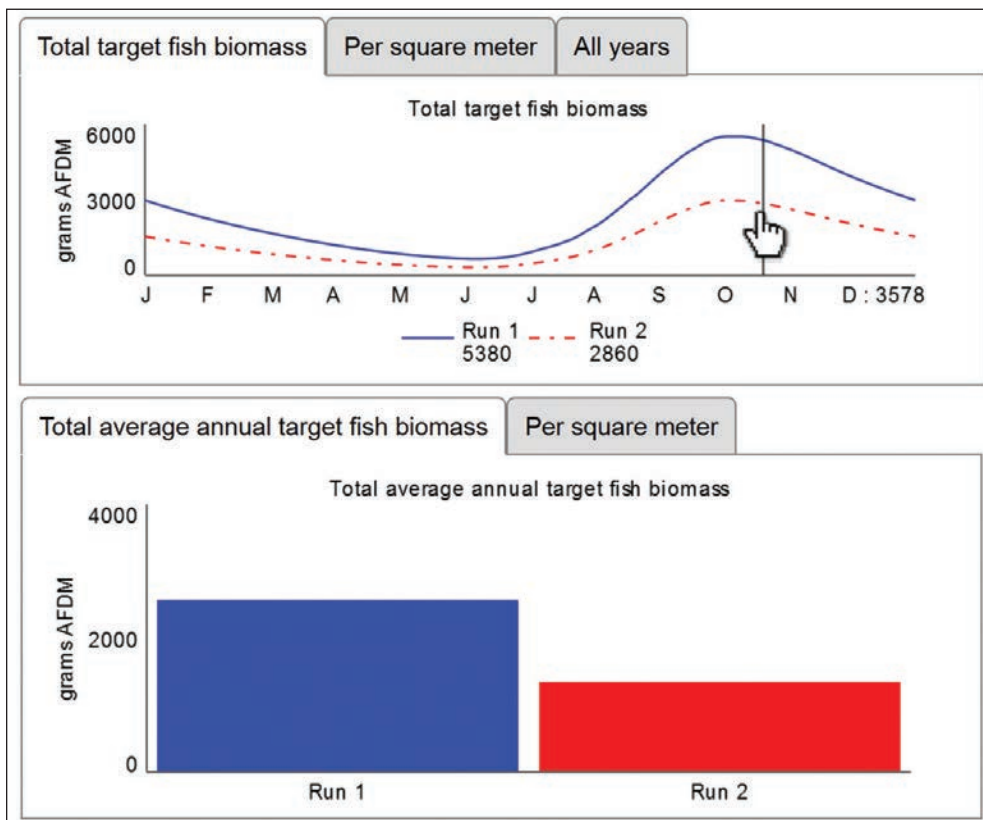


Figure 10—Example of output graphs. Click on the line or bar to display the value of the modeled variable at specific time steps. Use the tabs to view the stock biomass by the total biomass in the modeled reach or by biomass per square meter of the reach.

2.3 Parameterizing the ATP Model

2.3.1 Parameter Types

There are two groups of parameters in the ATP model: environmental and model parameters. Environmental parameters represent the physical, chemical, and biological conditions of the modeled reach (table 2), i.e., the environmental conditions that users input into the model to parameterize it for a given reach of interest. These parameters can be adjusted from the Interface. There are several different types of environmental parameters. “Constant” parameters have values that do not change through time. “Temporally dynamic” parameters are those, such as discharge and water temperature, that change in value through time and require users to input values for different days, weeks, or months of the year (depending on data availability). The default input for dynamic parameters is one calendar year of data. The model cycles through these inputs for each year of the simulation. Parameters described as “graphical function inputs” have a value that depends on the value of another parameter in the model. For instance, average channel width and water depth are dependent on discharge (see section 3.2.1, “Hydraulic Model Information”); the model searches the value of these parameters at a given time step based on user-specified relationships between width/depth and discharge. Some parameters may have multiple values to represent conditions in the main channel and an optional side channel.

In contrast to environmental parameters, model parameters are not specific to a reach. These parameters include the coefficients and exponents that govern the relationships between environmental conditions and the rates at which biomass flows into and out of stocks (see appendix for a list of model parameters and sources). For example, the model parameter, θ_F , is a temperature coefficient that describes the shape of the exponential relationship between temperature and the rate of respiration for fish. Model parameters are constants that can be adjusted only from the model window of Stella Architect. The values of these parameters are generally derived from published literature sources, although some parameter values are “assumed” based on model calibration (Bellmore et al. 2017). Advanced users with access to Stella Architect may wish to manipulate these parameters to evaluate how uncertainty in model parameter values influences simulation results.

Table 2—Environmental parameters that can be manipulated in the Aquatic Trophic Productivity model, including parameter units and variable types

Category	Parameter name	Units	Variable type
Channel hydraulics and morphology	Reach length ^a	Meters	Constant
	Channel slope ^a	Meter per meter	Constant
	Discharge	Cubic meters per second	Temporally dynamic
	One-dimensional rating curve relating discharge and average wetted width ^a	Meters	Graphical function input
	One-dimensional rating curve relating discharge and average water depth ^a	Meters	Graphical function input
	One-dimensional rating curve relating discharge and average proportion of wetted area suitable for target fish ^a	Meters	Graphical function input
	Substrate size distribution	Cumulative distribution	Graphical function input
	Side channel present?	Unitless	Constant (0 or 1)
	Side channel proportion of flow	Proportion	Constant
	Default side channel to main channel water depth ratio	Proportion	Constant
Water chemistry and temperature	Default side channel to main channel wetted width ratio	Proportion	Constant
	Water temperature	°C	Temporally dynamic
	Soluble reactive phosphorus concentration	Milligrams per liter	Temporally dynamic
	Dissolved inorganic nitrogen concentration	Milligrams per liter	Temporally dynamic
Solar inputs	Nephelometric turbidity	NTU	Temporally dynamic
	Sunlight (photosynthetically active radiation)	Moles per square meter	Temporally dynamic
	Proportion of stream shaded	Proportion	Temporally dynamic
Riparian conditions	Proportion of stream covered by vegetation ^a	Proportion	Constant
	Proportion of riparian vegetation that is deciduous	Proportion	Constant
	Proportion of riparian vegetation that is coniferous	Proportion	Constant
	Leaf-litter input per square meter of deciduous vegetation	Grams AFDM per square meter per year	Annual
	Leaf-litter input per square meter of coniferous vegetation	Grams AFDM per square meter per year	Annual
	Mean time of deciduous leaf fall	Julian day	Constant
	Standard deviation of leaf-fall time	Day	Constant

Table 2—Environmental parameters that can be manipulated in the Aquatic Trophic Productivity model, including parameter units and variable types (continued)

Category	Parameter name	Units	Variable type
Returning salmon spawners	Terrestrial invertebrate input per square meter of vegetation	Grams AFDM per square meter per year	Annual
	Mean time of terrestrial invertebrate input	Julian day	Constant
	Standard deviation of terrestrial invertebrate input	Day	Constant
	Returning salmon ^a	Salmon per year	Annual
	Mean arrival time of salmon at spawning ground	Julian day	Constant
	Standard deviation of salmon arrival time	Day	Constant
	Experimentally added salmon carcasses ^a	Salmon per year	Constant
	Day of carcass augmentation	Julian day	Constant
	Female fecundity	Eggs/female salmon	Constant
	Salmon egg mass	Grams AFDM/egg	Constant
Initial conditions	Salmon wet mass	Grams wet mass/salmon	Constant
	Proportion of carcass biomass stranded in terrestrial habitats	Proportion	Constant
	Target fish initial biomass	Grams AFDM per meter of reach length	Constant
	Nontarget fish initial biomass	Grams AFDM per meter of reach length	Constant
Food web conditions	Aquatic invertebrate initial biomass	Grams AFDM per meter of reach length	Constant
	Periphyton initial biomass	Grams AFDM per meter of reach length	Constant
	Fish competitors and predators present?	Unitless	Constant (0 or 1)

NTU = nephelometric turbidity units; AFDM = ash-free dry mass. We use AFDM because it eliminates the variability stemming from water content and allows comparisons among trophic levels.

^a Parameter inputs include values for the main channel and an optional side channel value.

2.3.2 Environmental Parameter Descriptions

Users can manipulate numerous environmental parameters to represent a range of physical, chemical, and biological conditions. Table 2 summarizes the environmental parameters that can be manipulated directly from the Interface or from the import spreadsheet. The parameter values used in the built-in model example are found in table 3. Some parameters (noted in footnote *a* in table 2) accept multiple values to represent conditions in the main channel and an optional side channel. For instance, users can input channel hydraulic information for both the main channel and a side channel. The section below includes detailed descriptions of the parameters. Parameters that can be manipulated only from the spreadsheet and not from the Interface are noted as “spreadsheet inputs.”

2.3.2.1 Detailed parameter descriptions (in alphabetical order)—

- **Aquatic invertebrate initial biomass (spreadsheet input)**
This parameter sets the initial biomass of aquatic invertebrates on the first day of the model simulation, in units of grams of AFDM per meter of reach length. This value is multiplied by the reach length in meters to calculate the initial biomass for the entire modeled river reach. The model is pre-coded with a background value for this parameter that is suitable for most conditions. This parameter should only be adjusted if the model is not reaching equilibrium dynamics (see section 1.6, “How the ATP Model Runs”).
- **Channel length**
Lengths of the main and optional side channel of the modeled river reach (m).
- **Channel slope**
Average water surface slope (m/m, 0–0.1) of the main and optional side channel of the modeled river reach.
- **Cumulative substrate size distribution**
The proportion (0–1) of the substrate that is smaller than the critical substrate size (m). The graph is used as a search function: the model selects the appropriate proportion of the substrate being mobilized for a given critical substrate size (i.e., the size of sediment that is actively mobilized at a given time step).
- **Day of carcass augmentation**
Julian day (1–365) when salmon carcasses are experimentally added to the stream.

Table 3—Values and sources of environmental parameters for the built-in model example

Parameter	Initial value	Source
Reach length (main and side channel)	619.5 m	USDI BOR 2012, 2015
Channel slope (main and side channel)	0.004 m/m	USDI BOR 2012, 2015
Discharge	Figure 20	Mastin 2015
One-dimensional rating curve relating discharge and average wetted width	Figure 21	USDI BOR 2012, 2015
One-dimensional rating curve relating discharge and average water depth	Figure 21	USDI BOR 2012, 2015
One-dimensional rating curve relating discharge and average proportion of wetted area suitable for target fish	Figure 21	USDI BOR 2012, 2015
Default side channel to main channel water depth ratio	0.5	Assumed
Default side channel to main channel wetted width ratio	0.2	Assumed
Cumulative substrate size distribution	0.064 m	CHaMP, median substrate size (D50) of distribution
Water temperature	Figure 20	CHaMP
Soluble reactive phosphorus concentration	Figure 20	Zuckerman 2015
Dissolved inorganic nitrogen concentration	Figure 20	Zuckerman 2015
Nephelometric turbidity	Figure 20	Zuckerman 2015
Sunlight (photosynthetically active radiation)	Figure 20	USDA 2013
Proportion of the stream shaded	Figure 20	CHaMP
Proportion of stream covered by vegetation	0.005	Calculated assuming 1 m overhang per bank and average width
Proportion of riparian vegetation that is deciduous	0.9808	CHaMP
Proportion of riparian vegetation that is coniferous	0.0192	CHaMP
Leaf-litter input per square meter of deciduous vegetation	104.5 g AFDM/m ² /year	Bellmore 2011. Assumes 5 percent ash content of litter samples. Connors and Naiman 1984, Muto et al. 2009.
Leaf-litter input per square meter of coniferous vegetation	323 g AFDM/m ² /year	Bellmore 2011. Assumes 5 percent ash content of litter samples. Connors and Naiman 1984, Muto et al. 2009.
Terrestrial invertebrate input per square meter of vegetation	10 g AFDM/m ² /year	Bellmore et al. 2013
Returning salmon (main channel)	15 salmon/year	Benjamin and Bellmore 2016, Snow et al. 2013. Assumes density of 0.001 salmon/m ² .
Salmon egg mass	0.03 g AFDM/egg	Quinn 2005
Salmon wet mass	5000 g wet mass/salmon	Quinn 2005
Female fecundity	3,900 eggs/female salmon	Quinn 2005
Proportion of salmon carcass biomass stranded in terrestrial habitats	0.2	Assumed

AFDM = ash-free dry mass.

- **Discharge**

Streamflow (m^3/s) through the modeled river reach. The default temporal resolution of this parameter is daily (Julian day 1 to 365); however, the user can increase or decrease the temporal resolution—from daily values to an annual value—depending upon data availability.

- **Experimentally added salmon carcasses**

The number of salmon carcasses added experimentally each year. Main and side channel inputs can be manipulated from the Interface.

- **Female fecundity**

Average fecundity of a female salmon (eggs/female).

- **Fish competitors present?**

Use the switch on the Interface or indicate on the import spreadsheet to add a stock of non-target fish that compete with juvenile salmon and trout (target fish).

- **Fish predators present?**

Use the switch on the Interface or indicate on the import spreadsheet to add a stock of non-target fish that act as predators of juvenile salmon and trout (target fish).

- **Leaf litter input from a square meter of coniferous vegetation (spreadsheet input)**

Annual coniferous leaf litter input ($\text{g AFDM}/\text{m}^2/\text{year}$). May be species specific or represent mixed coniferous vegetation.

- **Leaf litter input from a square meter of deciduous vegetation (spreadsheet input)**

Annual deciduous leaf-litter input ($\text{g AFDM}/\text{m}^2/\text{year}$). May be species specific or represent mixed deciduous vegetation.

- **Mean arrival time at spawning ground**

Mean arrival day (Julian day 1 to 365) that adult salmon enter the modeled river reach.

- **Mean time of deciduous leaf fall (spreadsheet input)**

Mean time (Julian day 1 to 365) of peak deciduous leaf abscission.

- **Mean time of terrestrial invertebrate input (spreadsheet input)**

Mean time (Julian day 1 to 365) of peak terrestrial invertebrate input to the stream.

- **Nitrogen [background dissolved nitrogen concentration]**

The background dissolved inorganic nitrogen (DIN) concentration of stream water (mg/L). Value represents the summation of nitrate (NO_3), nitrite (NO_2), and ammonium (NH_4). These numbers do not include nutrient inputs from

salmon, which are added to give the “total nitrogen concentration” value. The default temporal resolution of this parameter is monthly; however, the user can increase or decrease the temporal resolution—from daily values to an annual value—depending upon data availability.

- **Non-target fish initial biomass (spreadsheet input)**

This parameter sets the initial biomass of non-target fish on the first day of the model simulation, in units of grams of AFDM per meter of reach length. This value is multiplied by the reach length in meters to calculate the initial biomass for the entire modeled river reach. The model is pre-coded with a background value for this parameter that is suitable for most conditions. This parameter should only be adjusted if the model is not reaching equilibrium dynamics (see section 1.6, “How the ATP Model Runs”).

- **Periphyton initial biomass (spreadsheet input)**

This parameter sets the initial biomass of periphyton on the first day of the model simulation, in units of grams of AFDM per meter of reach length. This value is multiplied by the reach length in meters to calculate the initial biomass for the entire modeled river reach. The model is pre-coded with a background value for this parameter that is suitable for most conditions. This parameter should only be adjusted if the model is not reaching equilibrium dynamics (see section 1.6, “How the ATP Model Runs”).

- **Phosphorus [background dissolved phosphorus]**

The background soluble reactive phosphorus (SRP) concentration in stream water (mg/L). These numbers do not include nutrient inputs from salmon, which are added to give the “total phosphorus concentration” value. The default temporal resolution of this parameter is monthly; however, the user can increase or decrease the temporal resolution—from daily values to an annual value—depending upon data availability.

- **Proportion of deciduous vs coniferous vegetation**

The proportion (0–1) of riparian canopy cover that is deciduous and the proportion that is coniferous (sum to 1).

- **Proportion of salmon carcass biomass stranded in terrestrial habitats**

The proportion (0–1) of salmon carcass biomass (from spawners and added salmon) that is stranded in terrestrial habitats, such as gravel bars.

- **Proportion of stream covered by vegetation**

The proportion (0–1) of the main and optional side channel covered by riparian vegetation.

- **Proportion of stream shaded**

The proportion (0–1) of the above-canopy photosynthetically active radiation (PAR) that is blocked from reaching the surface of the water because of shading by topography (e.g., canyon walls) or riparian vegetation that can be determined from a hemispherical canopy photo. The default temporal resolution of this parameter is monthly; however, the user can increase or decrease the temporal resolution—from daily values to an annual value—depending upon data availability.

- **Proportion of wetted area suitable for fish**

Graphical relationship between discharge and the proportion of the wetted area suitable for fish. The graph is used as a search function: the model selects the appropriate proportion of suitable area for the main or side channel at a given discharge. The proportion of suitable area can be determined using “habitat suitability indices” (HSIs) that relate the suitability of a given location in the stream to water depth and velocity. For instance, if water depth is too shallow or velocity is too fast for the target fish species, then that specific location of the stream would be considered “unsuitable.” These inputs can be obtained from a detailed hydraulic model of the reach (see section 3.1.1.1, “Hydraulic model information”). Although the ATP model represents the “averaged” conditions for entire river reaches, fishes perceive suitable habitat at much finer spatial scales. Thus, determining the proportion of habitat that is suitable for fish may require summarizing information for more spatially explicit two- or three-dimensional hydraulic models.

The side channel graphical function is a customized side channel feature and is blank by default. To use this feature, the user must first enter data in the table of the side channel graphical function or import data from the import spreadsheet.

Without a customized side channel, the default side channel proportion of wetted area suitable for juvenile salmon and trout is 0.5 (constant value).

- **Proportional increase in wetted area suitable for fish**

Increases the proportion (0–1) of the main channel wetted area suitable for fish by modifying the HSIs. Such an increase may occur with restoration activities designed to increase the quality and quantity of the habitat. An increase of 0.5 converts 50 percent of the unsuitable area to suitable area, and a 100 percent increase results in all the wetted area being suitable for fish. The default value of 0 means that there is no change from the values in the graphical function for the proportion of wetted area suitable for fish.

- **Returning salmon**

Number of adult salmon returning to spawn in the modeled reach per year. This number is held constant through the simulation and does not change in response to model manipulations.

- **Salmon egg mass**
Mean mass of a salmon egg (grams of AFDM).
- **Salmon wet mass**
Mean wet mass of a spawning salmon (grams of wet mass).
- **Side channel present?**
Toggle to turn on and off a side channel.
- **Side channel to main channel water depth ratio**
Without side-channel-specific hydraulic curves, the hydraulics of the default side channel are based on a relationship between the side channel and main channel. For example, if the side channel to main channel water depth ratio is 0.5, then the water depth in the side channel will be 50 percent of the main channel depth.
- **Side channel to main channel wetted width ratio**
Without side-channel-specific hydraulic curves, the hydraulics of the default side channel are based on a relationship between the side channel and main channel. For example, if the side channel to main channel wetted width ratio is 0.2, then the side channel wetted width will be 20 percent of the main channel width.
- **Standard deviation of arrival time**
The standard deviation, in days, around the mean time of adult salmon return.
- **Standard deviation of leaf-fall time (spreadsheet input)**
The standard deviation, in days, around the mean time of peak deciduous leaf abscission.
- **Standard deviation of terrestrial invertebrate input time (spreadsheet input)**
The standard deviation, in days, around the mean time of peak terrestrial invertebrate input to the stream.
- **Sunlight**
Empirical estimate of the above-canopy PAR (the light available for photosynthesis in mol/m^2). The default temporal resolution of this parameter is daily (Julian day 1 to 365); however, the user can increase or decrease the temporal resolution—from daily values to an annual value—depending upon data availability.
- **Target (juvenile) fish initial biomass (spreadsheet input)**
This parameter sets the initial biomass of fish on the first day of the model simulation, in units of grams of AFDM per meter of reach length. This value is multiplied by the reach length in meters to calculate the initial biomass for the

entire modeled river reach. The model is pre-coded with a background value for this parameter that is suitable for most conditions. This parameter should be adjusted only if the model is not reaching equilibrium dynamics (see section 1.6, “How the ATP Model Runs”).

- **Terrestrial invertebrate input per a square meter of vegetation (spreadsheet input)**

Annual terrestrial invertebrate input from a square meter of riparian vegetation (g AFDM/m²/year).

- **Turbidity**

Average nephelometric turbidity (in NTUs) of the stream water. The default temporal resolution of this parameter is monthly; however, the user can increase or decrease the temporal resolution—from daily values to an annual value—depending upon data availability.

- **Water depth**

Graphical relationship between discharge (m/s³) and the average water depth (m) of the main channel or side channel. The graph is used as a search function: the model selects the appropriate average water depth for the channel at a given discharge. These inputs can be obtained from a detailed hydraulic model of the reach (see section 3.1.1.1, “Hydraulic model information”).

The side channel graphical function is a customized side channel feature and is blank by default. To use this feature, the user must first enter data in the table of the side channel graphical function or import data from the import spreadsheet.

- **Water temperature**

Average daily water temperature (°C). Default input is one calendar year of data (Julian day 1 to 365). The temperature regime is held constant through each simulation but can be adjusted between model runs.

- **Wetted width**

Graphical relationship between discharge (m/s³) and the average wetted width (m) of the main or side channel. The graph is used as a search function: the model selects the appropriate average wetted width for the channel at a given discharge. These inputs can be obtained from a detailed hydraulic model of the reach (see section 3.1.1.1, “Hydraulic model information”).

The side channel graphical function is a customized side channel feature and is blank by default. To use this feature, the user must first enter data in the table of the side channel graphical function or import data from the import spreadsheet.

2.3.3 Model Parameterization Overview

Although the ATP model comes parameterized with environmental conditions for an existing river reach, most users will wish to reparameterize the model to represent a given reach of interest. Users can do this by modifying the environmental conditions on the Interface or by importing data from a Microsoft Excel™ import spreadsheet.

2.3.3.1 How to customize the model—

The following directions describe how to customize the ATP model for a different river reach.

1. Determine if the ATP model is the appropriate tool for the river reach in question (see section 1.5.4, “Fundamental Assumptions”).
2. Identify which environmental conditions (parameters) need to be adjusted to parameterize the model for the new reach. See section 2.3.4, “Model Outputs,” for a list and description of these parameters. The model user may initially choose not to adjust some parameters. For example, the user may choose to use the built-in value for female salmon fecundity if reach-specific data are unavailable.
3. Format the data so that the units match those listed. Check that values fall within the accepted ranges for the parameter (e.g., channel slope should be between 0 and 0.1).
4. Modify the input values on the Interface (see section 2.3.3.2, “Interface parameter manipulations”) or by importing the data from a comma-separated value (CSV) file (see section 2.3.3.3, “Importing data”).
5. Run the model from the Interface to simulate the background conditions of the reach (see section 2.2, “Navigating the Model Interface”).
6. Examine how sensitive the model is to changes in these background environmental conditions to verify that these parameter values make sense (see section 2.4.1, “Reach-Specific Dynamics”).
7. Manipulate the physical and/or biological conditions of the reach for different scenarios (e.g., a side channel addition) and examine the change in fish biomass (see section 2.4, “Model Manipulations”).
8. Export simulation data to capture results for further analysis and documentation (see section 2.3.4.1, “Exporting data”).

2.3.3.2 Interface parameter manipulations—

The user can reparameterize the model by individually manipulating the input values for one or more of the parameters on the Interface (see section 2.2, “Navigating the Model Interface,” for instructions on using the input devices). Note that changes

made to parameters are not saved when the input devices are restored. Parameter values are held constant through the simulation; these values cannot be adjusted during the simulation.

2.3.3.3 Importing data—

The user can input their own data by using the “Import” button on the **Simulation** tab on the Interface. This function imports environmental parameter values from a CSV file into the model, temporarily overriding the values used in the built-in model example (see section 2.1, “Model Access and Compatibility,” for details on saving changes). Importing data from a CSV file is an efficient way to reparameterize the model using data for a specific reach of interest. A link to an Excel import spreadsheet, populated with the values used in the built-in model example, is available on the **Simulation** tab. There are two sheets within the import spreadsheet file: “ATP Model Input” and “Formatted Input.” Before importing, the user will need to save the “Formatted Input” sheet as a CSV (or tab-delimited) file.

On the first sheet named “ATP Model Input,” users can enter data for the environmental parameters in the blue boxes under the different headings, such as reach characteristics or terrestrial inputs (fig. 11). For example, the length of the

[illegible]

Figure 11—"ATP Model Input" sheet of the import spreadsheet showing a subset of the environmental inputs (including shading, water chemistry and temperature, and the substrate size) used to parameterize the model for a specific reach. ATP = Aquatic Trophic Productivity.

modeled main channel in meters can be entered in cell B6. Users should enter their data in the units listed to avoid model errors. Descriptions of the parameters listed in the spreadsheet can be found in section 2.3.2.1, “Detailed parameter descriptions.” Additionally, the spreadsheet contains parameter-specific notes indicated by the red triangle in the upper righthand corner of the spreadsheet cell. To fully parameterize the model for a river reach, the user should enter values for all of the listed parameters. However, users can choose to update a subset of input parameters depending on available data and assumptions. Users can enter data at a higher temporal resolution (up to daily values) or a lower resolution than the initial values used for the built-in model example. When coarser temporal resolution data are used, the model extrapolates a daily parameter value from the values provided. To use a different number of values for a parameter than the number used in the built-in model example, no additional formatting is required on the part of the user. However, when importing the data, users will receive a warning message that the model is changing the number of points for the variable. The second sheet in the Excel file, the “Formatted Input” sheet, puts all user-inserted parameter values (from the “ATP Model Input” sheet) into a format that can be read by the Stella software. Model users do not need to make any edits to this sheet, which is “locked” to prevent users from unintentionally modifying inputs. Changes made to the input values or temporal resolutions of parameters on the first sheet will be automatically formatted for import into the ATP model.

To import data into the ATP model:

1. Open the Excel import spreadsheet (download link available on the Interface).
2. Enter reach-specific data for each parameter in the labeled column in the correct units and update the temporal resolution in Julian days (or substrate size for the substrate size distribution) as needed.
3. Save any changes to the spreadsheet.
4. Use "Save As" to save the “formatted input” sheet as a CSV file.
5. From the Interface, click “Import data” and select a file to import.
6. Review any messages produced by the import. If the user changes the temporal resolution of parameters, a message will indicate that the model is “Changing the number of points from X to XX for the variable [name];” however, no further action is needed.
7. Run the model and review parameter values to check for parameterization errors (see sections 2.4.1, “Reach-Specific Dynamics,” and 2.5, “Troubleshooting”).

2.3.4 Model Outputs

Numerous potential outputs from the ATP model can be tailored to the user's question. The current Interface focuses on the results for the target fish stock. The main **Simulation** page summarizes the dynamics of the target fish stock with both a line graph and a bar graph (fig. 12). The line graph displays the temporal dynamics of the target fish stock for the last year of the 10-year model run (once biomass levels have equilibrated), and the bar graph displays the average annual biomass for the target fish stock (also for the final year of the model run). Both these graphs are comparative and display the results for up to nine model runs. Line graphs showing the temporal biomass dynamics of other food web members (deciduous and coniferous detritus, periphyton, aquatic invertebrates, and non-target fish) can be viewed via the "Other food web members" button on the main **Simulation** page (fig. 13). Quantitative comparisons between model runs (beyond visualizing differences between runs in the graphs) must be done outside of the Interface. Export links can be established from the Interface that allow users to export the biomass values for all food web members to a CSV file for further analysis (see 2.3.4.1, "Exporting data").

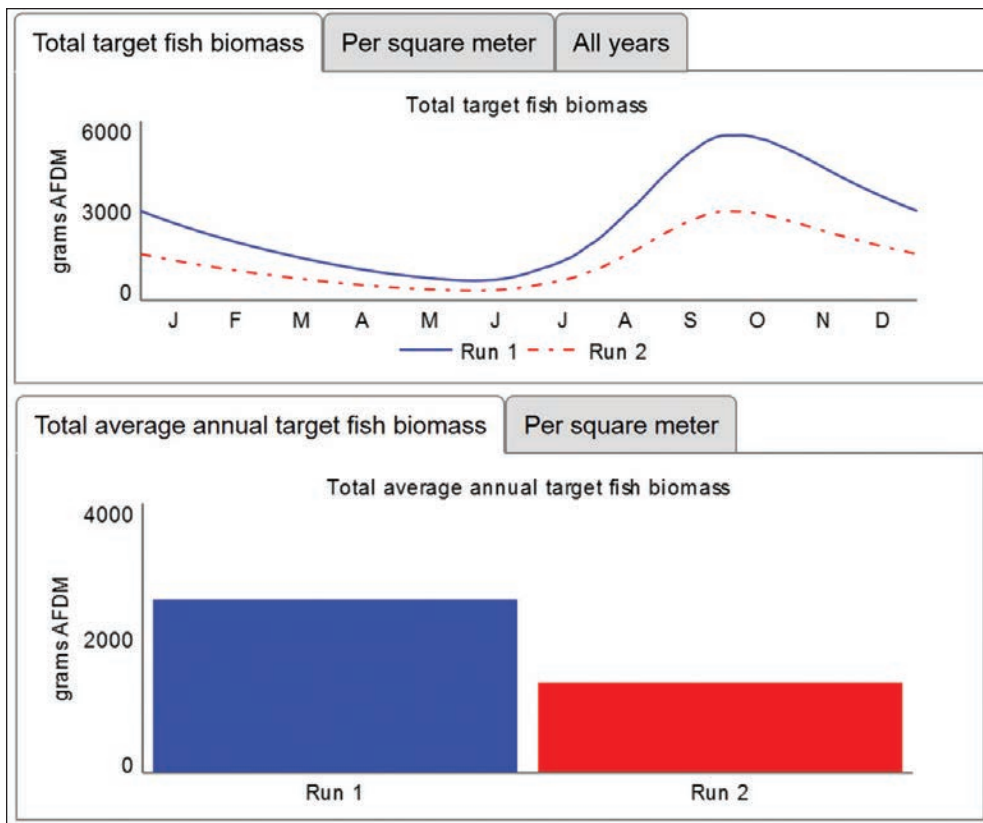


Figure 12—Target fish biomass graphs that display the average annual fish biomass and the temporal dynamics of fish biomass during the final year of the simulation, after the model has equilibrated. AFDM = ash-free dry mass.

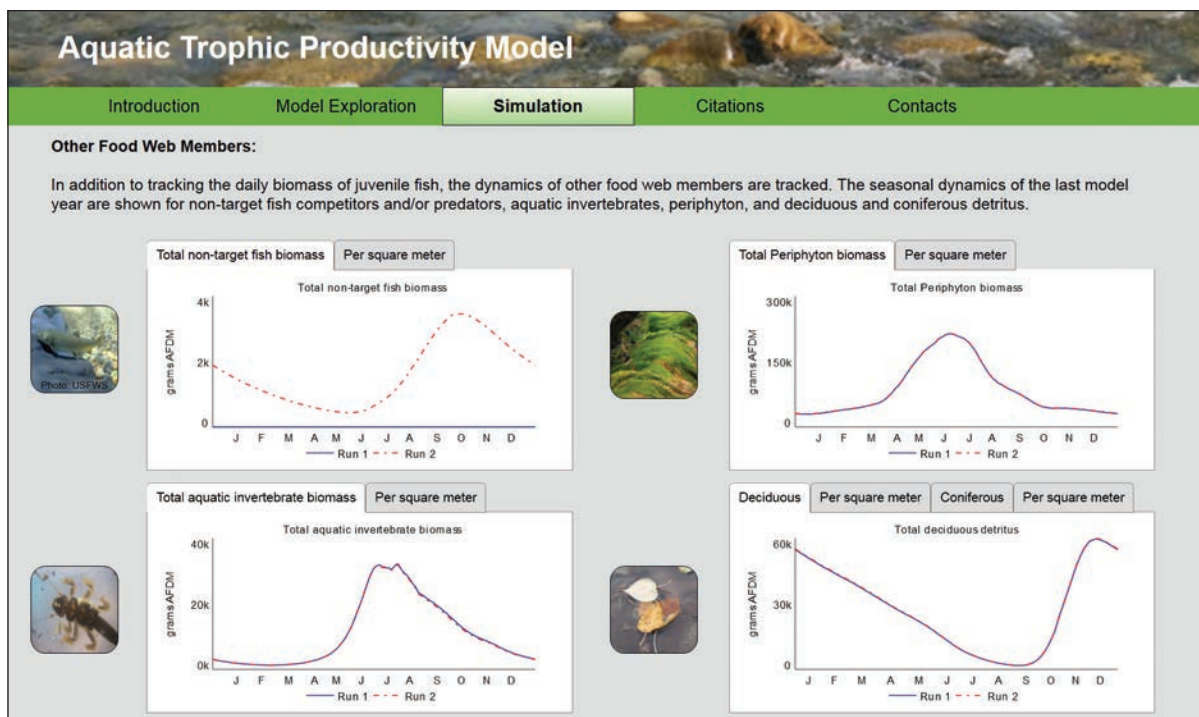


Figure 13—Interface page showing the biomass dynamics of other food web members, including non-target fish, aquatic invertebrates, periphyton, and deciduous and coniferous detritus. Under background conditions (run 1, solid blue line), non-target fish are absent and the biomass remains at zero. Fish competitors and predators were turned on for run 2 (dashed red line). AFDM = ash-free dry mass.

2.3.4.1 Exporting data—

Users can export parameter values using the “Export” button on the **Simulation** tab. This button pastes the biomass values of target fish, non-target fish, aquatic invertebrates, periphyton, and terrestrial detritus from the last simulation into a CSV file. To compare outputs across simulations, the user should export data after each model run.

2.4 Model Manipulations

The ATP model Interface can be used to explore the current conditions of the river reach as well as the response of fish biomass to manipulations of the physical or biological conditions of the reach (see section 1.4, “Model Applications”). There are a number of ways in which the model can be manipulated from the Interface, several of which are described below. These are by no means the only ways to use the Interface; the user can independently adjust a number of model parameters either simultaneously or across a series of model runs. Users may contact the authors if they wish to run more complex simulations than can be done from the Interface. See section 3.1, “Model Manipulation Example,” for step-by-step directions on model manipulations using the built-in model example.

2.4.1 Reach-Specific Dynamics

By parameterizing the model with data for an individual river reach (see section 2.3.3.2, “Interface parameter manipulations”), the ATP model can be used to simulate background biomass dynamics of fishes, as well as the other members of the food web (periphyton, terrestrial detritus, and aquatic invertebrates). Additionally, users can conduct exploratory analyses to examine how sensitive the model is to changes in these background environmental conditions. For example, model users can adjust nutrient concentrations, water temperatures, discharge, stream shading, and leaf litter (as well as many other factors) to see how the biomass dynamics of fish and other food web members respond to these changes, either individually or in combination. We strongly encourage model users to conduct these informal sensitivity analyses prior to conducting more structured analyses. Informally gaming the model in this way helps users understand the dynamics of the model, as well as identify potential errors in model parameterization. Moreover, these preliminary analyses can be used to identify the types of manipulations that are most likely to achieve desired outcomes (e.g., increased fish biomass). Model users may also wish to parameterize the ATP model for multiple locations within or across watersheds and use the model to explore the unique factors that control/limit production at each location.

2.4.2 Food Web Manipulations

Previous analyses using the model illustrate that the dynamics of the model can be strongly sensitive to adding or subtracting species from the food web (Bellmore et al. 2017). The model Interface allows users to manipulate the structure of the food web via the addition of a non-target stock of fishes that both competes for food with, and preys upon, the target juvenile salmon and trout stock. The biomass of this non-target fish stock is displayed on the “Other Food Web Members” page accessed via the main **Simulation** tab. Observe that adding the stock of non-target fish affects the dynamics not only of target fish but also the dynamics of the other food web members.

This stock is meant to represent the community of native and nonnative fishes with which juvenile salmon and trout frequently interact. In the Pacific Northwest, for example, this might include native species such as sculpin (*Cottus* spp.), mountain whitefish (*Prosopium williamsoni*), and adult bull trout (*Salvelinus confluentus*), and nonnative species such as smallmouth bass (*Micropterus dolomieu*) and brook trout (*S. fontinalis*). The addition of these non-target fishes can significantly influence the modeled biomass of target fish. Users **should not** misinterpret this modeled result as an indication that populations of other fishes need to be controlled or eliminated. These communities of fishes occur naturally in many watersheds,

and although they **may** reduce the carrying capacity for a given desired species, they likely contribute to the long-term stability and resilience of the ecosystem (Bellmore et al. 2015, Thibaut and Connolly 2013). Despite the potential for misinterpretation of model results, we chose to allow users to add/remove this non-target fish stock because these simulations can provide insights into how differences in the structure of food webs influence responses to alternative management actions. Thus, we encourage model users to run a range of management actions with the non-target fish stock turned on and off.

2.4.3 Side Channel Addition

The Interface includes the option to add a side channel to the modeled river reach. This feature allows model users to explore restoration efforts aimed at reconnecting or recreating floodplain aquatic habitats, or, if the modeled reach already contains a side channel, to code this side channel into the model. Toggling the “side channel present” switch on the **Simulation** tab turns on a side channel. By default, this side channel receives 10 percent of the total discharge (value cannot be manipulated). The side channel length and slope are initially set equal to that of the main channel. The side channel wetted width and depth are set to be a proportion of the main channel width and depth. The user can adjust these default fractions, as well as the length and proportion of side channel wetted area suitable for fish on the “Side channel hydraulics” page accessed from the **Simulation** tab.

Alternatively, customized side channels can be parameterized into the model if detailed hydraulic information is available for a preexisting or proposed side channel. By turning on the “Use side channel hydraulic curves” switch on the “Side channel hydraulics” page, model users can enter graphical functions that describe the relationship between reach discharge and channel width, average water depth, and the proportion of wetted area that is suitable for fish. Customized hydraulic information for the side channel can also be uploaded using the import spreadsheet.

2.4.4 Habitat Suitability Manipulations

The proportion of the wetted area of the modeled main channel suitable for fish can be manipulated to simulate changes in habitat quality and quantity, i.e., changes to the proportion of habitat that has depths and velocities that are suitable for the target fish species. Changes to suitable habitat could occur with any restoration strategy that changes the hydraulics of the channel, such as placement of large woody debris or rock weirs. On the Interface, habitat suitability can be manipulated by sketching a new curve for the “proportion of wetted area suitable for fish” graphical function. This curve describes the relationship between discharge and the proportion of habitat that is suitable for fish at that discharge. For instance, habitat

suitability may decrease with increasing discharge because of higher water velocities that are no longer suitable for fish; alternatively, habitat suitability may increase with discharge because of the lateral expansion of the channel onto floodplain surfaces that have lower velocities. This type of information can be summarized from the outputs of two- or three-dimensional hydraulic models (see section 3.1.1.1, “Hydraulic model information”).

Alternatively, model users can adjust this relationship by manipulating the “proportional increase in wetted area suitable for fish” numeric input on the main **Simulation** tab. Adjusting this numeric input only modifies habitat suitability in the main channel of the modeled reach; it does not affect the suitability of the side channel, if present. Increasing the value of this numeric input above 0 converts “unsuitable” habitat to “suitable” habitat. For example, setting the value of this input to 0.5 converts 50 percent of the unsuitable wetted area to suitable area, and a value of 1.0 results in all the wetted area being suitable for fish.

2.4.5 Marine-Derived Nutrient Manipulations

The amount of marine-derived nutrients entering the modeled river reach can be adjusted to explore the food web consequences of smaller or larger salmon returns. In addition, model users can augment the modeled reach with dead salmon to represent management actions that intentionally add salmon carcasses (or similar salmon “analog” material) (Bilby et al. 1998, Kohler et al. 2012) to rivers. The number of returning salmon and augmented salmon carcasses can be adjusted on the main **Simulation** tab using the numeric inputs in the “Marine inputs” box. Users can also click on the “Additional controls button” to adjust other parameters relating to salmon inputs. Specifically, users can adjust body mass, arrival time, and fecundity of returning salmon spawners to represent different salmon species, or even other anadromous and semelparous fish (i.e., organisms that die following spawning, such as Pacific lamprey). Moreover, if a side channel is present in the modeled reach, users can adjust the number of spawning salmon returning (or number of carcasses added) to this habitat. All these environmental parameters can also be imported to the model using the import spreadsheet. Note: added salmon carcasses do not contain eggs and are added as a pulse into the system on a single day specified by the user. These carcasses are added each year of the 10-year model simulation.

2.4.6 Riparian Vegetation Manipulations

The Interface allows users to independently modify both the proportion of the stream covered by vegetation and the proportion of the stream that is shaded. Manipulating these parameters affects the lateral inputs of terrestrial organic matter (coniferous and deciduous leaf litter and invertebrates) and the amount of sunlight

reaching the streambed, respectively. These environmental inputs can be adjusted to represent riparian management actions such as riparian planting, or alternatively, logging/thinning of trees in riparian zones. Both these parameters can be adjusted on the main **Simulation** tab. Click on the “Additional controls” button for terrestrial inputs to adjust the proportion of riparian vegetation that is coniferous versus deciduous, as well as the amount of vegetation cover for the optional side channel habitat. It is important to note that changes to the proportion of the stream covered by riparian vegetation do not influence bank stability, large woody debris contributions, or water temperature. However, these effects could be incorporated into model simulations by independently altering the “proportion of wetted area that is suitable for fish” (to represent more/less woody debris in the channel) or “water temperature” (to represent more/less solar radiation reaching the stream).

2.5 Troubleshooting

This section includes symptoms and solutions for potential problems that may be encountered when using the Interface and manipulating (importing) parameter values. For more general help, see ISEE Systems’ help pages (<https://www.iseesystems.com/resources/help/v1-6/default.htm>).

Symptom: The Interface does not accept a change to a numeric input (value is reset).

Solution: If the new value is outside the accepted input range, the numeric input will reset to the maximum or minimum allowable value, whichever is closer. For example, if a value of 100 is entered for a parameter with an input range of 0 to 1, the parameter value will be set to 1. Check that the value is within the accepted range (listed in parentheses after the parameter name).

Symptom: Changes to background nutrient concentrations on the “Stream Conditions” page do not affect the periphyton growth rate displayed on the graph.

Solution: The growth rate of periphyton is only influenced by the most limiting nutrient (either dissolved inorganic nitrogen or soluble reactive phosphorus) at a given time step (see section 4.2.1, “Periphyton Production”). If the changes made to the nutrient concentrations do not change the nutrient that is most limiting, the effect of nutrients on the growth rate will not change.

Symptom: An alert is triggered during the simulation indicating that equilibrium has not been reached. This alert appears if the average annual target fish biomass in year 10 of the simulation is not within 1 percent of the value for year 9 of the simulation. Equilibrium can also be visually assessed by examining the graph of all 10 years of target fish biomass dynamics shown in the third tab of the target fish biomass line

graph on the **Simulation** tab of the Interface. If the target fish biomass dynamics fluctuate between years, it is an indication that equilibrium has not yet been reached.

Solution: If the target fish biomass is still decreasing as indicated by the pop-up message, the user should decrease the initial target fish biomass on the import spreadsheet and rerun the simulation. If the target fish biomass is increasing, the user can increase the initial biomass of target fish. Users can also reduce the time it takes for the biomass dynamics to equilibrate by adjusting the initial biomass values of non-target fish, aquatic invertebrates, and periphyton from the import spreadsheet (see section 2.3.2.1, “Detailed parameter descriptions”).

Symptom: After importing data via an import spreadsheet, the model does not behave as expected.

Solution: Check the parameter values in the model against the import spreadsheet to see if the data imported correctly. Changes to the options selected on the import dialogue box can affect how values are imported (see section 2.3.3.3, “Importing data”). Finally, ensure that the changes to the Excel spreadsheet were saved as a CSV file before importing data. Using the import button imports the last saved version of the CSV file.

Symptom: When importing data, the message “Failed to find any variables in... Expecting format: a,b 1,2” appears.

Solution: Check that the file selected for import was a CSV file and not an Excel file.

Symptom: When importing data using an import spreadsheet, the message “Failed to import the value ‘X’ for the variable ‘Y’ because the value is outside of the input range specified” appears.

Solution: Check that the input value falls within the input range listed after the parameter name on the Interface or under the parameter description (see section 2.3.2.1, “Detailed parameter descriptions”).

Symptom: The graphical functions for the side channel are blank (or have values of zero). Clicking on the graph does not produce a line.

Solution: Data for side-channel-specific graphical functions are not built into the model. The default side channel shown in the Interface does not use side-channel-specific graphical functions and instead calculates side channel widths and depths as a proportion of those found in the main channel and assumes that the proportion of wetted area suitable for fish is constant. To create a custom side channel, see section 2.4.3, “Side Channel Addition.”

Symptom: After parameterizing the model with the user's own data, the graphical function graphs appear cut off along the Y-axis rendering some or all of the data not visible.

Solution: The axis range of the graphs is set according to the data values of the built-in model example. If the user's values are outside this range, they may not be visible on the graph. The user can see and manipulate the values by clicking on "Table" in the upper right-hand corner of the graph window. Alternatively, users with Stella Architect can adjust the axis ranges from the model window.

Chapter 3: Built-In Model Example

Even without entering any data, the user can run the model and adjust parameters to explore the target fish biomass response to different environmental conditions or restoration actions using the built-in model example. For this application, the ATP model was parameterized with environmental conditions for a mid-size (5th order) salmon-bearing stream, or more specifically, a reach in the Methow River watershed in north-central Washington state, USA. Located on the lower Chewuch River, a tributary to the Methow River, this reach is a part of the Columbia Habitat Monitoring Program (CHaMP; site CBW05583-347417). CHaMP is a monitoring program in the Columbia River basin (<https://www.champmonitoring.org>).

3.1 Model Manipulation Example

As discussed in section 2.4, “Model Manipulations,” there are a variety of manipulations that can be conducted from the Interface. For instance, the model could be used to explore responses to the following three manipulations, an increase in habitat suitability, marine-derived nutrients, and riparian vegetation. When these actions are simulated, the comparative graphs on the Interface can be used to examine the responsiveness of the modeled river reach to the manipulations. Step-by-step directions for running each of these simulations, (using the built-in model example data and version 3.3 of the model), are presented below.

1. Background conditions: Click “Run model” without changing any of the built-in parameter values to run a simulation based on background conditions (fig. 14, run 1).
2. Increase in habitat suitability: Simulate an increase in habitat suitability by setting the “proportional increase in wetted area suitable for fish” input equal to 1.0 from the main **Simulation** tab. This represents a scenario in which 100 percent of the main channel wetted area is suitable for fish, which affects the biomass density of target fish and their consumption rate. Alternatively, instead of inputting a proportional increase, the model user could click on “Additional controls” in the main channel hydraulics box on the **Simulation** tab and trace a line equal to 1.0 for the “proportion of wetted area suitable for fish” graphical function. This scenario looks at the maximum possible increase associated with projects designed to increase habitat quality and quantity; however, in reality, it is not feasible to create a channel that is 100 percent suitable for fish. After making one of these changes, click “Run model.” The average annual fish biomass increased in response to this change (fig. 15, run 2).

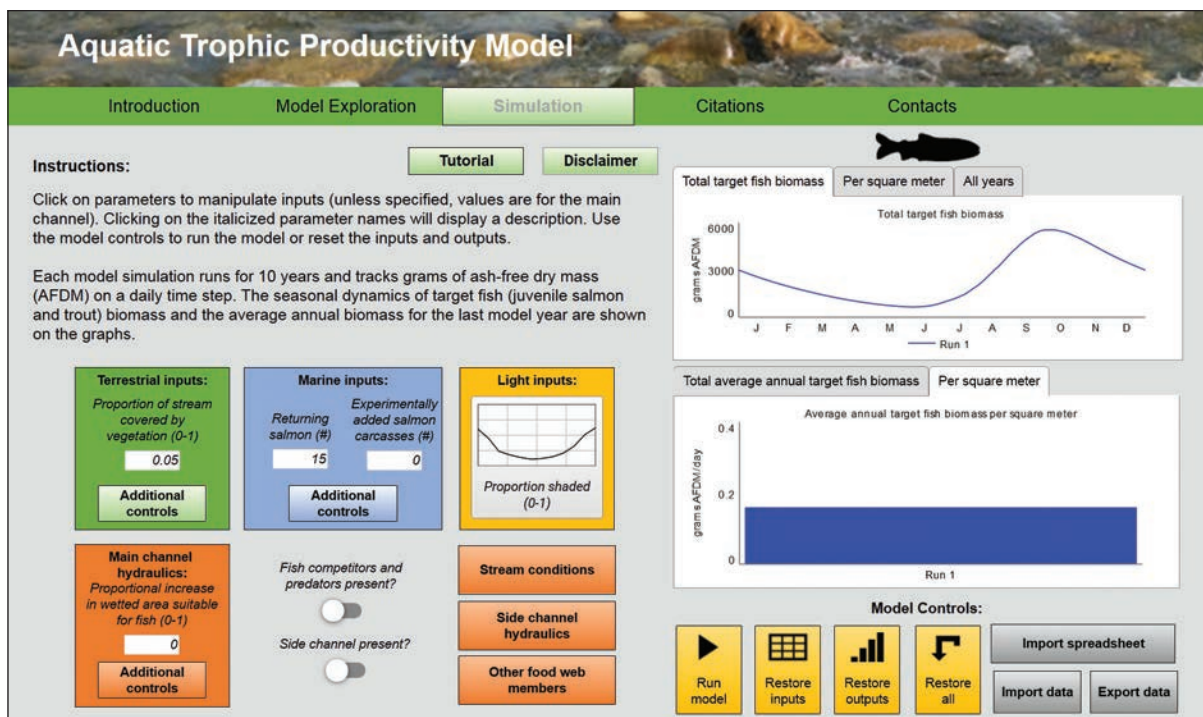


Figure 14—Interface screen showing settings to simulate background conditions (run 1).

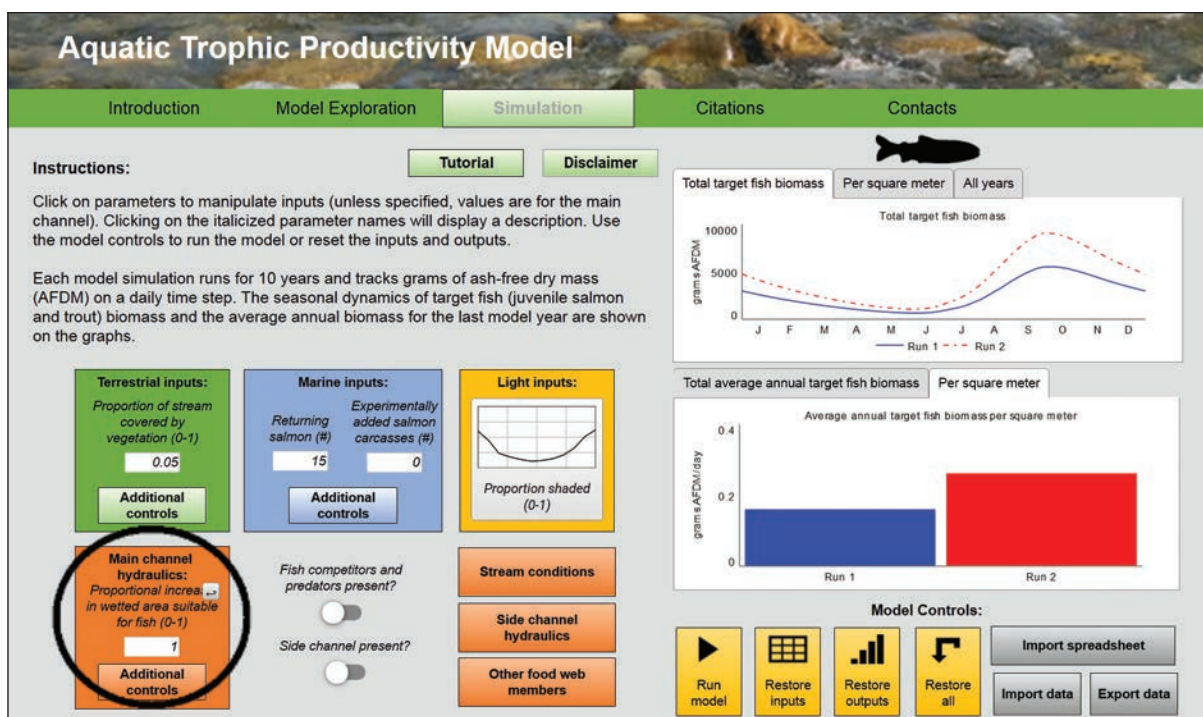


Figure 15—Interface screen showing settings to simulate an increase in habitat suitability (run 2).

- Click “Restore inputs” to reset the proportion of wetted area suitable for fish to the built-in parameter value before running the next simulation (fig. 16). The comparative graphs will remain.

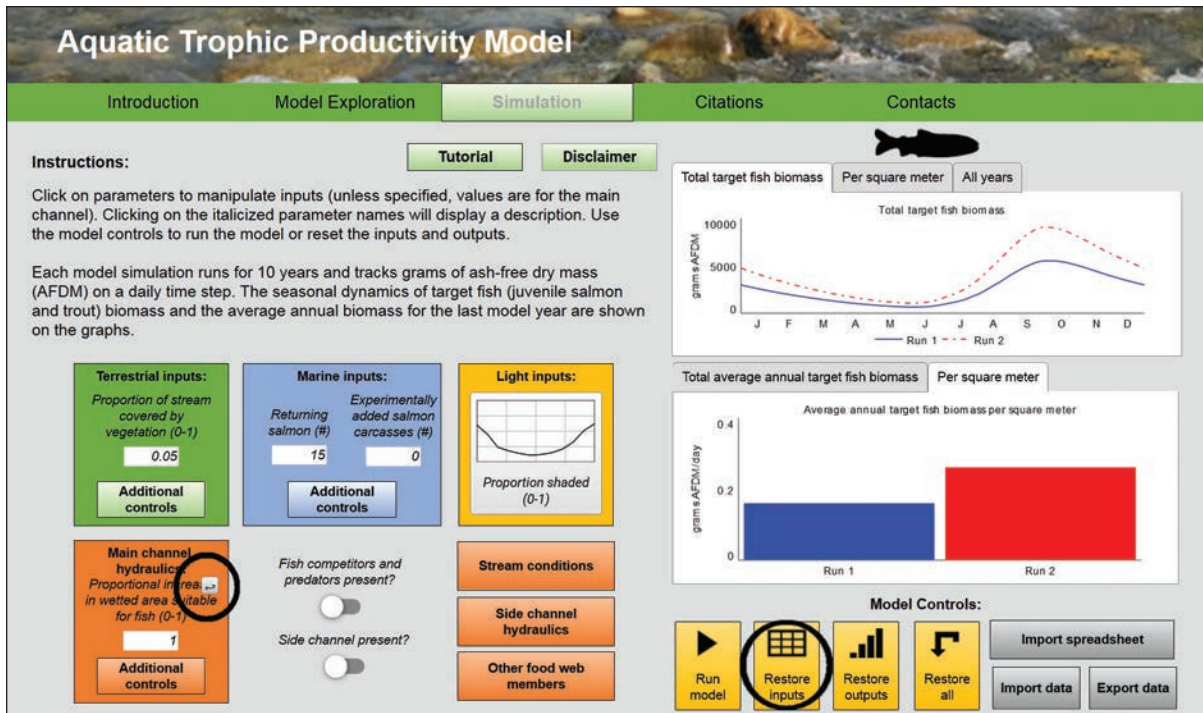


Figure 16—Interface screen highlighting the “restore inputs” and the individual reset buttons, either one of which can be used to reset inputs between simulations.

- Increase in marine-derived nutrients: Simulate an increase in marine-derived nutrients by experimentally adding salmon carcasses. On the **Simulation** tab, under marine inputs, type 300, which is equal to 20 times the current number of returning salmon (15 salmon/year), into the “experimentally added carcasses” parameter input. This change will affect the food resources available to aquatic invertebrate and fish consumers as well as stream nutrient concentrations. Click “Run model.” The average annual fish biomass increased relative to background conditions but decreased compared to run 2 (fig. 17, run 3).

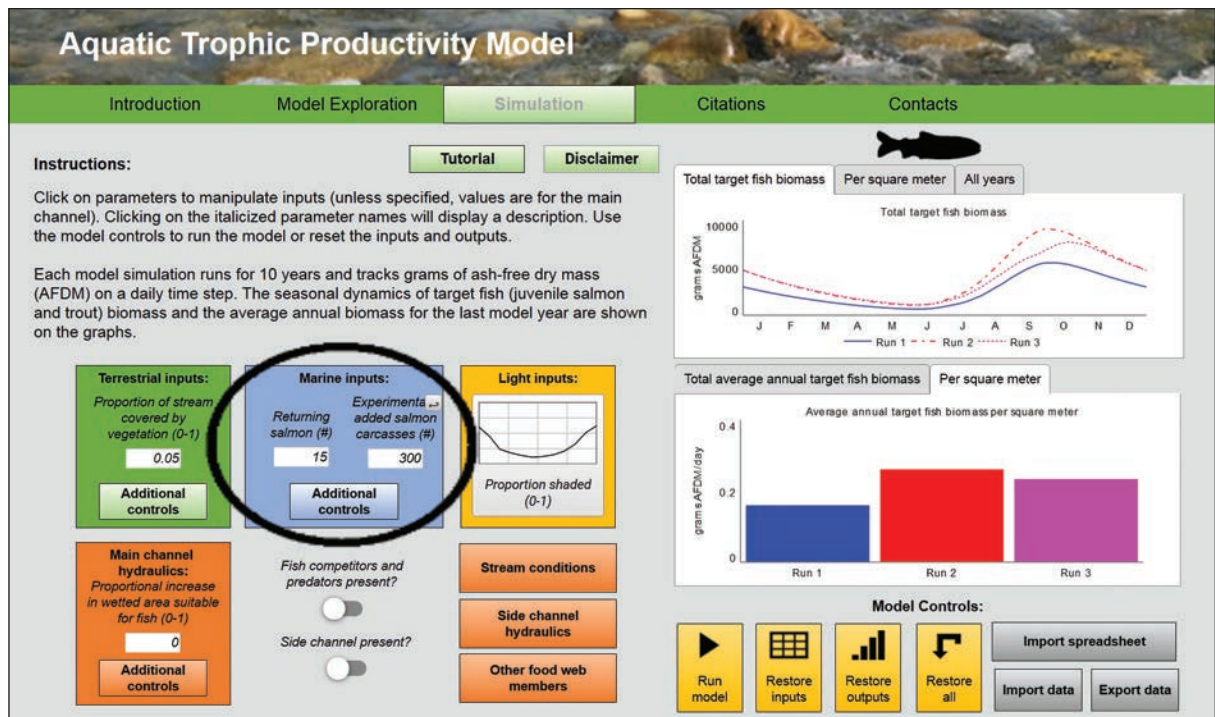


Figure 17—Interface screen showing settings to simulate an increase in marine-derived nutrients (run 3).

- Click “Restore inputs” to reset the number of added salmon carcasses. The value should reset to zero.
- Increase in riparian vegetation: Simulate an instantaneous doubling of riparian vegetation cover by manipulating the “proportion of stream covered by vegetation” numeric input found in the terrestrial inputs box on the main **Simulation** tab. Change this parameter value from 0.05 to 0.1 (5 percent cover to 10 percent cover). This scenario assumes that the added vegetation is mature and results in an increase in the input of both terrestrial detritus (leaf litter) and invertebrates. Click “Run model.” The average annual fish biomass decreased compared to run 3 (fig. 18, run 4). Note that this simulation does not change the proportion of the stream that is shaded. Shading can be independently adjusted from the “Light inputs” box on the main simulation page.

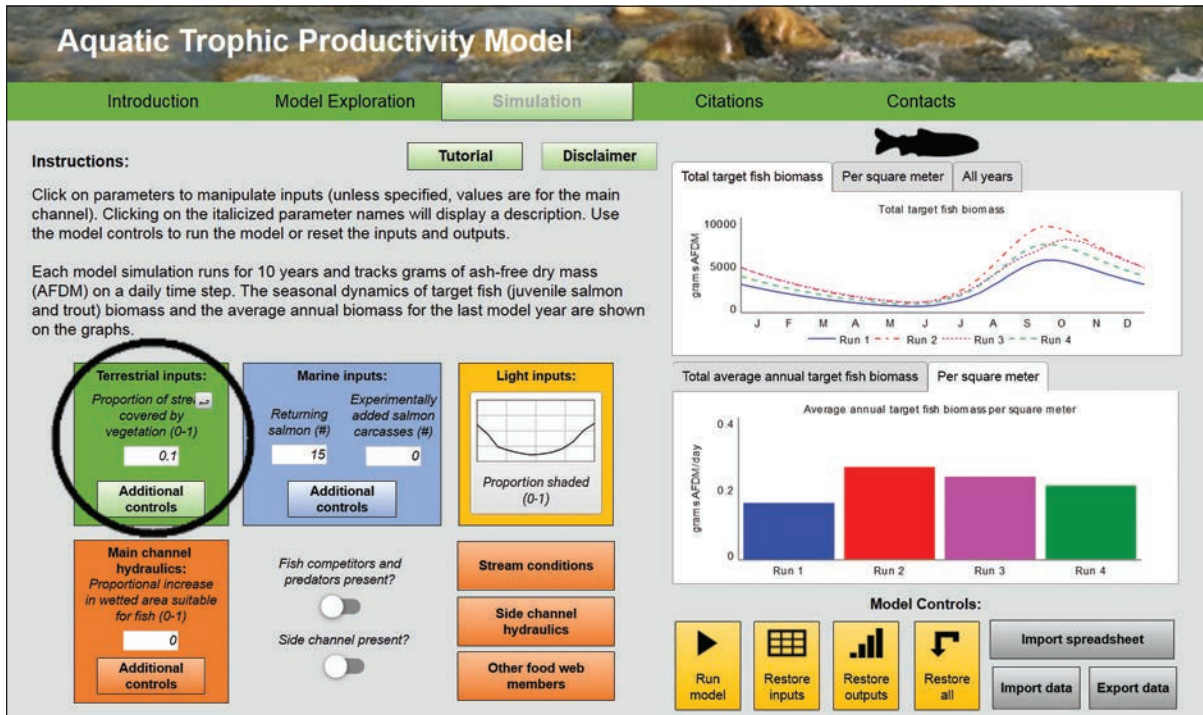


Figure 18—Interface screen showing settings to simulate an increase in riparian vegetation (run 4).

Under these conditions, target fish biomass at this reach increased with each of the manipulations (fig. 19). The reach was most sensitive, however, to an increase in habitat suitability (run 2).

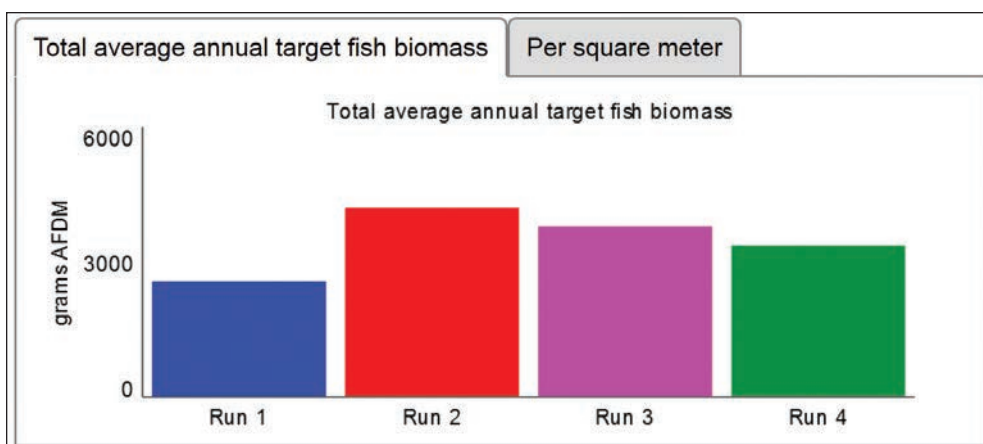


Figure 19—Built-in model average annual target fish biomass (g AFDM) under background conditions (run 1), increased habitat suitability (run 2), increased marine-derived nutrients (run 3), and increased riparian vegetation (run 4). AFDM = ash-free dry mass.

3.1.1 Built-In Model Environmental Parameter Data Sources

The data used to parameterize the ATP model for the built-in example came from a number of sources, including field data collection efforts, published literature, and reach-specific modeling projects. Table 3 lists the parameter sources and values (see fig. 20).

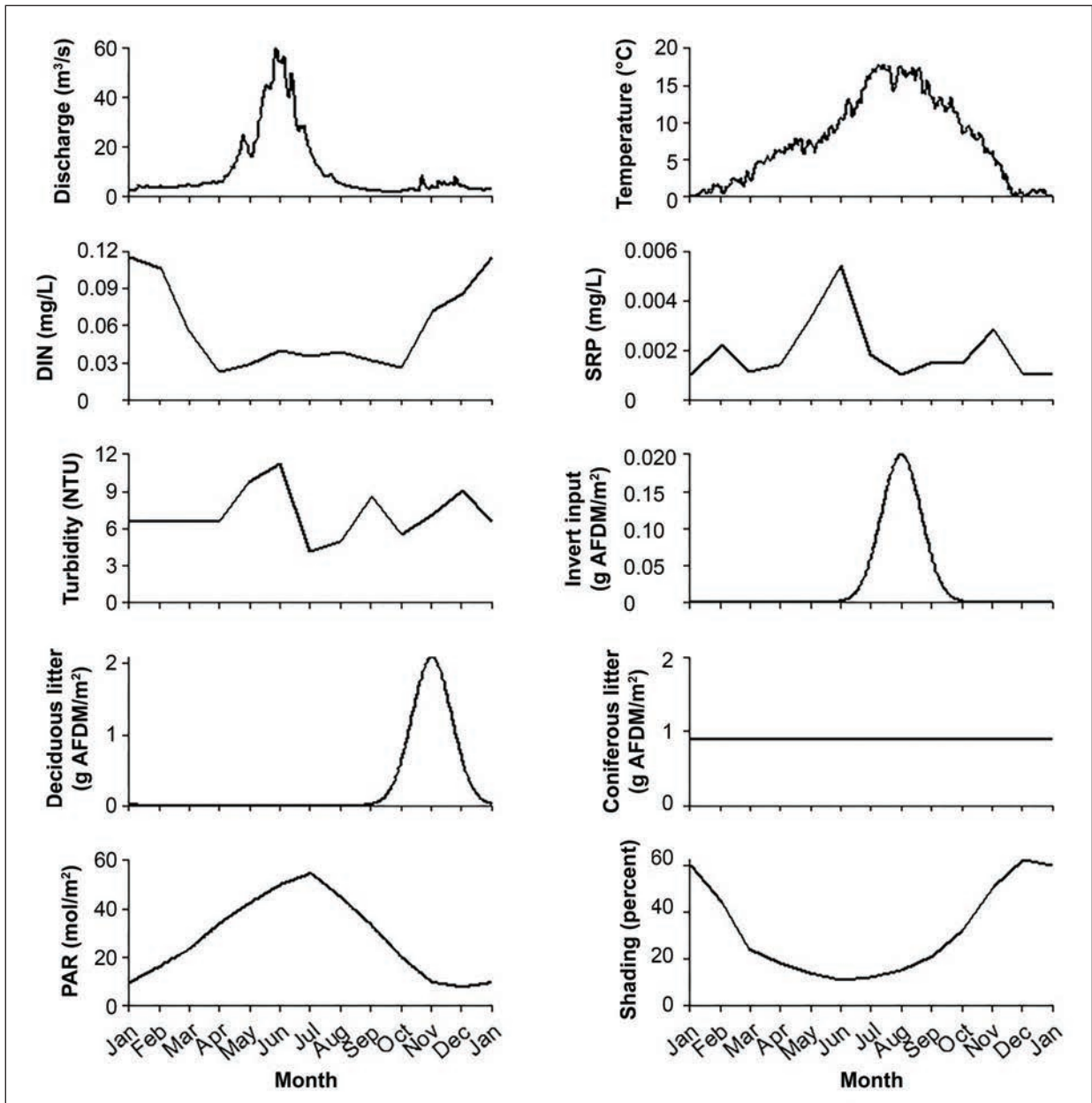


Figure 20—Temporally dynamic environmental inputs (see table 3 for sources). Discharge (total flow through modeled reach); temperature (water temperature); DIN (dissolved inorganic nitrogen); SRP (soluble reactive phosphorus); invert input (input of terrestrial invertebrates); deciduous litter (input of deciduous leaf litter [detritus]); coniferous litter (input of coniferous leaf litter [detritus]); PAR (photosynthetically active radiation); and shading (percentage of the reach shaded). AFDM = ash-free dry mass. NTU = nephelometric turbidity unit.

3.1.1.1 Hydraulic model information—

The hydraulic inputs used in the built-in model example (fig. 21) were calculated by summarizing the output of a two-dimensional hydraulic model that was run at a range of discharges that represent the annual hydrograph of the modeled reach (USDI BOR 2012, 2015) (fig. 22). Average wetted width was calculated by dividing the wetted area from the two-dimensional model run by the length of the reach measured along the main channel thalweg. Average water depth was calculated by averaging together the depths in each cell of the two-dimensional grid (fig. 22A), weighted by the area of each cell. Similar to depth, the percentage of the habitat that was suitable for fish at each modeled discharge was the weighted average of the suitability values from each cell in the two-dimensional grid, where the “suitability” of each cell was determined using depth and velocity suitability curves for juvenile Chinook salmon (Raleigh et al. 1986).

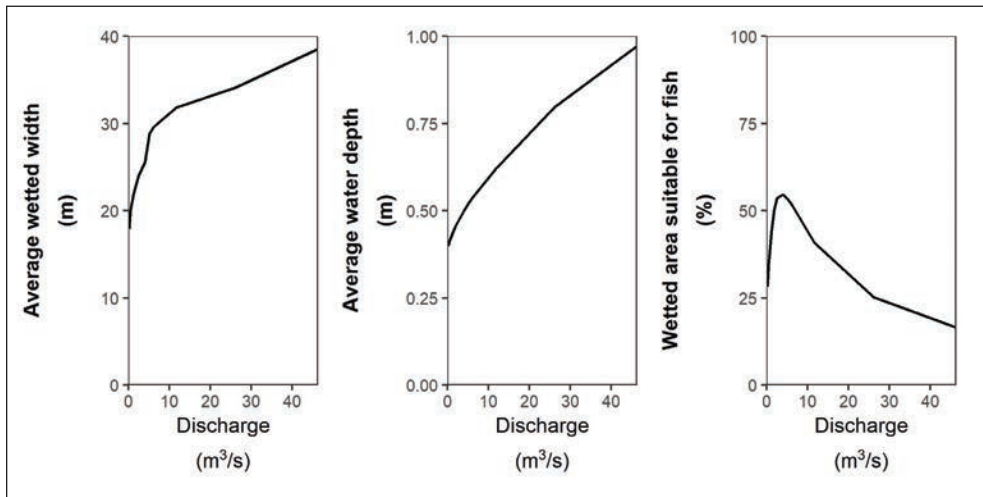


Figure 21—Hydraulic inputs for the built-in model example (see table 3 for sources). These one-dimensional rating curves describe the relationship between discharge and the average wetted width, water depth of the main channel, and proportion of the channel habitat suitable for target fish based on summarizing the results from a two-dimensional hydraulic model for the reach.

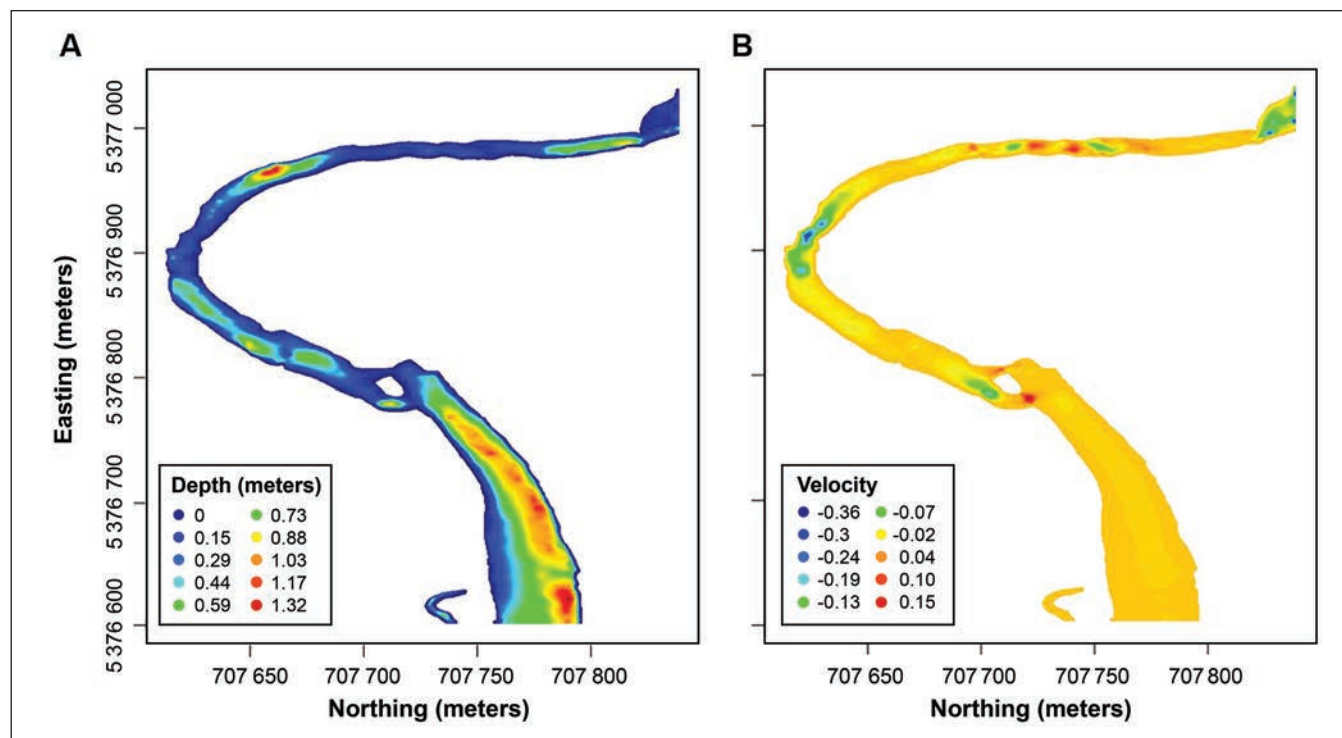


Figure 22—(A) Water depth (m) and (B) velocity (m/s) plots for a single discharge from the two-dimensional hydraulic model for the built-in example reach.

Chapter 4: Model Structure

The model is composed of first-order differential equations with a separate equation for each of the stocks in the model. The daily evaluation of these equations produces the biomass dynamics seen for each of the stocks. A time step (DT) of one day was selected for numerical accuracy (Ford 2010: 44). The mass balance equations for each stock are presented in table 4. Biomass stocks increase if the inflows that contribute to biomass gains (e.g., consumption and energy assimilation, upstream/lateral inputs, and production) outweigh the outflows that contribute to biomass losses (e.g., predation, downstream export, and respiration). For example, fish biomass (F) increases via inflows of consumed food resources, and decreases via outflows of respired energy, predation by non-target fishes, and background mortality. In the section below, we summarize the inflows and outflows that govern the dynamics of each biomass stock

Table 4—Mass balance equations for the biomass stocks in the Aquatic Trophic Productivity model

Stock	Mass balance equation
Target fish, F	$\frac{dF}{dt} = \text{Consumption}_{AF}\alpha_{AF} + \text{Consumption}_{TF}\alpha_{TF} + \text{Consumption}_{EF}\alpha_{EF} + \text{Consumption}_{SF}\alpha_{SF} - \text{Consumption}_{FN} - \text{Respiration}_F - \text{Mortality}_F \quad (1)$
Non-target fish, N	$\frac{dN}{dt} = \text{Consumption}_{AN}\alpha_{AN} + \text{Consumption}_{TN}\alpha_{TN} + \text{Consumption}_{EN}\alpha_{EN} + \text{Consumption}_{SN}\alpha_{SN} - \text{Consumption}_{FN} - \text{Respiration}_N - \text{Mortality}_N \quad (2)$
Aquatic invertebrates, A	$\frac{dA}{dt} = \text{Consumption}_{PA}\alpha_{PA} + \text{Consumption}_{DA}\alpha_{DA} + \text{Consumption}_{SA}\alpha_{SA} + \text{Upstream}_A - \text{Consumption}_{AN} - \text{Respiration}_A - \text{Mortality}_A - \text{Export}_A \quad (3)$
Terrestrial invertebrates, T	$\frac{dT}{dt} = \text{Lateral}_T + \text{Upstream}_T - \text{Consumption}_{TF} - \text{Consumption}_{TN} - \text{Decay}_T - \text{Export}_T \quad (4)$
Periphyton, P	$\frac{dP}{dt} = \text{Production}_P + \text{Upstream}_P - \text{Consumption}_{PA} - \text{Decay}_P - \text{Export}_P \quad (5)$
Terrestrial detritus, D_i	$\frac{dD_i}{dt} = \text{Lateral}_{D_i} + \text{Upstream}_{D_i} - \text{Consumption}_{D_iA} - \text{Decay}_{D_i} - \text{Export}_{D_i} \quad (6)$
Salmon eggs, E	$\frac{dE}{dt} = \text{Marine}_E + \text{Upstream}_E - \text{Consumption}_{EF} - \text{Consumption}_{EN} - \text{Decay}_E - \text{Export}_E \quad (7)$
Salmon carcasses, S	$\frac{dS}{dt} = \text{Marine}_S + \text{Upstream}_S - \text{Consumption}_{SA} - \text{Consumption}_{SF} - \text{Consumption}_{SN} - \text{Decay}_S - \text{Export}_S \quad (8)$

Note: α_{xy} is the proportion of prey type X consumed by predator Y that is assimilated. The terms in each equation represent the inflows and outflows of biomass from each stock and are described in section 4.2, “Inflows and Outflows.” Subscript definitions: F , target fish; N , non-target fish; A , aquatic invertebrates; T , terrestrial invertebrates; P , periphyton; D_i , terrestrial detritus, where i is either d , deciduous, or c , coniferous; S , salmon carcasses; E , salmon eggs.

(consistent with the **Model Exploration** tab on the Interface; section 4.1, “Stock Summaries”) and then we describe the mathematical form of the inflows and outflows and how these flows are linked to environmental conditions (section 4.2, “Inflows and Outflows”). Much of this information has been documented previously (Bellmore et al. 2014, 2017; Benjamin and Bellmore 2016) but is compiled here for reference.

4.1 Stock Summaries

4.1.1 Target Fish

This stock tracks the biomass of the “target” fish (F), which was so named because the bioenergetics parameters (e.g., consumption and respiration rates) that influence the dynamics of this stock were parameterized for juvenile trout and salmon, which are frequently the target or focal species of restoration actions. Advanced model users can adjust these bioenergetics parameters to represent a variety of fish species or size classes. Equation 1 in table 4 governs the dynamics of this stock. The stock and flow structure of the target fish stock is shown in figure 23 and described below.

- **Target fish organic matter assimilation:** Juvenile salmon and trout consume aquatic and terrestrial invertebrates as well as salmon eggs and carcasses. The assimilation of this organic matter increases target fish biomass and is a function of the quality and quantity of prey, water temperature,

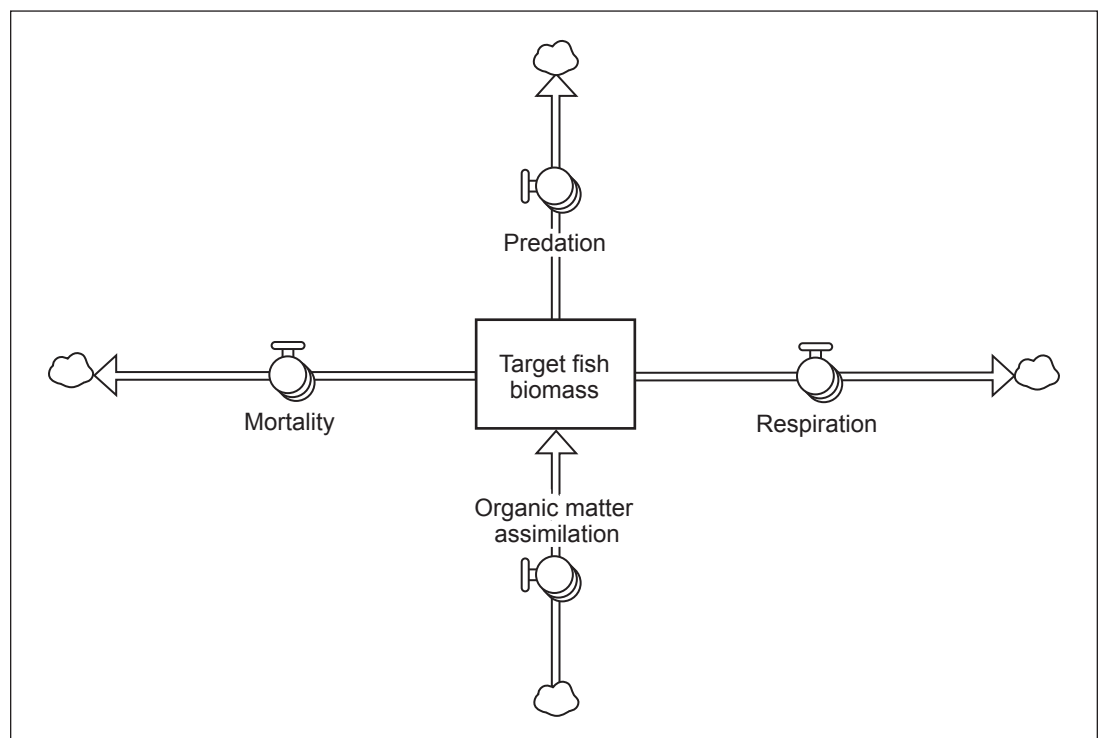


Figure 23—Stock and flow structure of the target fish stock.

and fish density. Foraging efficiency increases as prey (e.g., aquatic invertebrates) becomes more available, but declines as fish density increases owing to increased competition for food.

- **Target fish respiration:** Fish respiration represents the loss of biomass from metabolic processes. Respiration is assumed to increase exponentially with water temperature.
- **Target fish predation:** Predation represents the loss of juvenile salmon and trout to non-target fish predators that can be turned on and off in the model. Predation increases as the population of predators increases and as the availability of juvenile fish increases.
- **Target fish mortality:** Fish mortality represents the loss of biomass resulting from non-predation-induced natural mortality and is controlled by a constant rate.

4.1.2 Non-Target Fish

The stock of non-target fish (N) represents the biomass of a fish that can compete with and prey upon the target fish depending on model settings. When “Fish competitors and predators” are turned on from the Interface (or “competition/predation ON?” is set to 1 in the import spreadsheet), the stock of non-target fish competes with target fish for shared food resources and preys upon target fish. If “Fish competitors and predators” are turned off, the non-target fish biomass will remain at zero. Equation 2 in table 4 governs the dynamics of this stock. The stock and flow structure of the non-target fish stock is shown in figure 24 and described below.

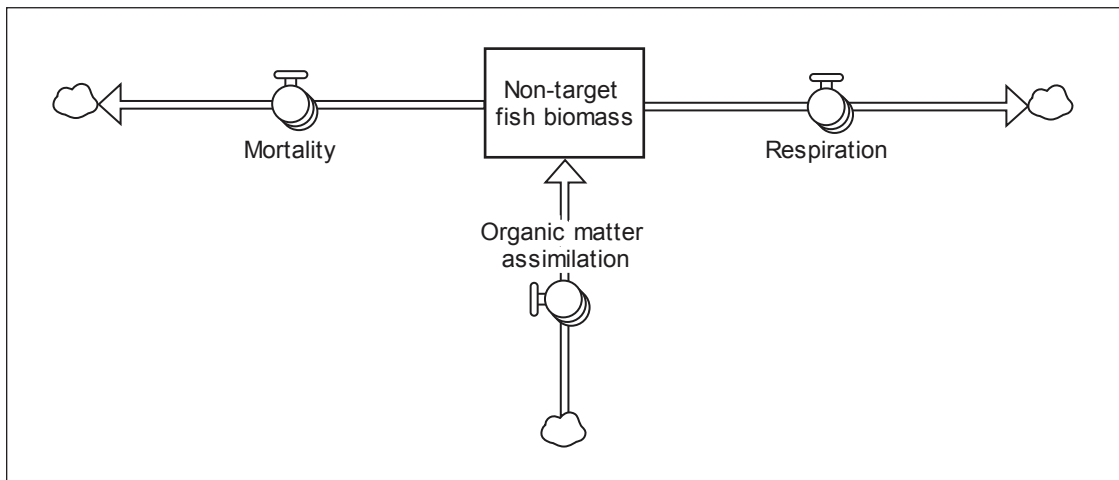


Figure 24—Stock and flow structure of the non-target fish stock.

- **Non-target fish organic matter assimilation:** Non-target fish can consume aquatic and terrestrial invertebrates, salmon eggs and carcasses, and target fish depending on food web controls. The assimilation of this organic matter increases non-target fish biomass and is a function of the quality and quantity of prey, water temperature, and fish density. Foraging efficiency increases as prey (e.g., aquatic invertebrates) becomes more available, but declines as non-target fish density increases owing to increased competition for food.
- **Non-target fish respiration:** Fish respiration represents the loss of biomass from metabolic processes. Respiration is assumed to increase exponentially with water temperature.
- **Non-target fish mortality:** Fish mortality represents the loss of biomass resulting from non-predation-induced natural mortality and is controlled by a constant rate.

4.1.3 Aquatic Invertebrates

The aquatic invertebrate stock (A) represents a generalized aquatic invertebrate assemblage. Equation 3 in table 4 governs the dynamics of this stock. The stock and flow structure of the aquatic invertebrate stock is shown in figure 25 and described below.

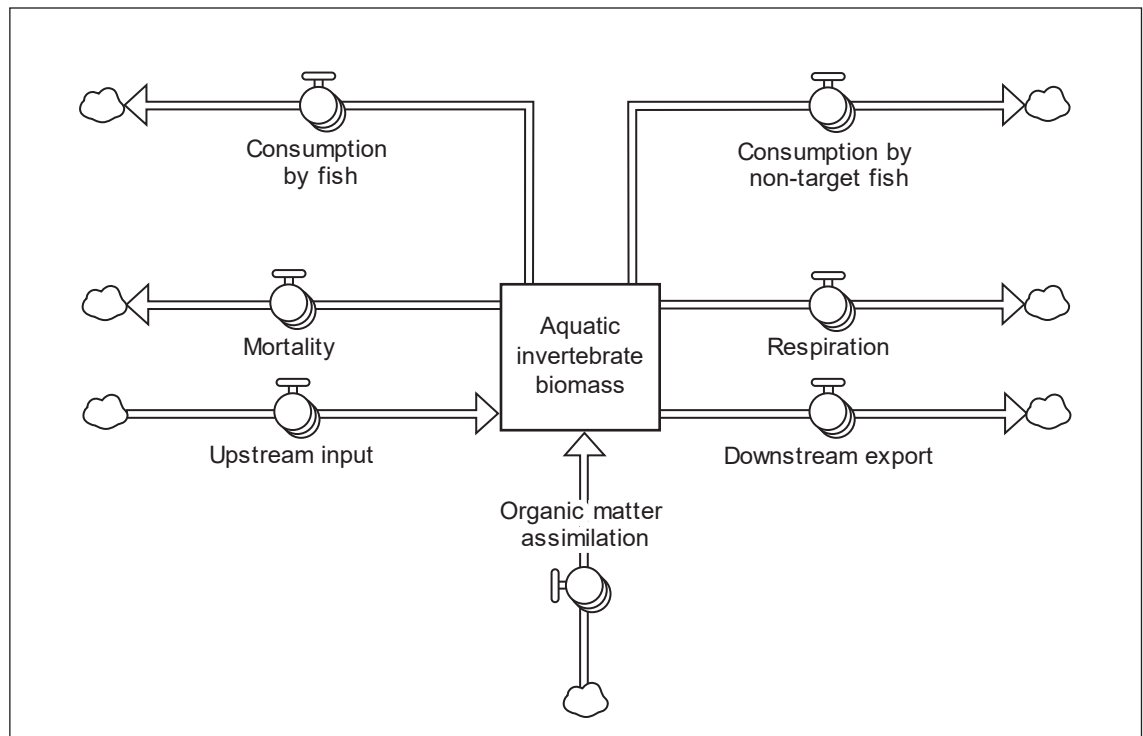


Figure 25—Stock and flow structure of the aquatic invertebrate stock.

- **Aquatic invertebrate organic matter assimilation:** Invertebrates consume periphyton, terrestrial detritus, and salmon carcasses. The assimilation of this organic matter increases invertebrate biomass and is a function of the quality and quantity of prey, water temperature, and invertebrate density. Foraging efficiency increases as food items (e.g., periphyton and leaf litter) become more available, but declines as invertebrate density increases owing to increased competition for food.
- **Aquatic invertebrate respiration:** Invertebrate respiration represents the loss of biomass from metabolic processes. Respiration is assumed to increase exponentially with water temperature.
- **Aquatic invertebrate mortality:** Invertebrate mortality represents the loss of biomass resulting from non-predation-induced natural mortality and is controlled by a constant mortality rate.
- **Aquatic invertebrate consumption:** Consumption represents the loss of invertebrate biomass to fish consumers. Consumption increases as the population of fish consumers increases and as the availability of invertebrates increases. A small proportion of the invertebrate biomass, the refuge biomass, is invulnerable to consumption and export (e.g., invertebrates in the hyporheic zone).
- **Aquatic invertebrate downstream export and upstream inputs:** Downstream exports represent the loss of invertebrate biomass to downstream reaches owing to hydraulic forces that scour the streambed and mobilize benthic organisms. As with consumption, there is a refuge biomass of invertebrates that is invulnerable to export. Upstream inputs represent the invertebrate biomass that is transported into the modeled reach from upstream.

4.1.4 Terrestrial Invertebrates

The terrestrial invertebrate stock (T) represents the biomass of terrestrial invertebrates in the modeled stream. Equation 4 in table 4 governs the dynamics of this stock. The stock and flow structure of the terrestrial invertebrate stock is shown in figure 26 and described below.

- **Terrestrial invertebrate lateral inputs:** Lateral inputs represent the input of invertebrates from adjacent riparian vegetation. These inputs are calculated within the import spreadsheet and are based on a normal distribution around a peak time of input. Salmon carcasses stranded in terrestrial habitats adjacent to the stream can attract a large number of terrestrial invertebrates, which can subsequently become prey for fish (Meehan et al. 2005, Scheuerell et al. 2007). To account for this, terrestrial inputs increase when carcasses are present (see section 4.1.8, “Salmon Carcasses”).

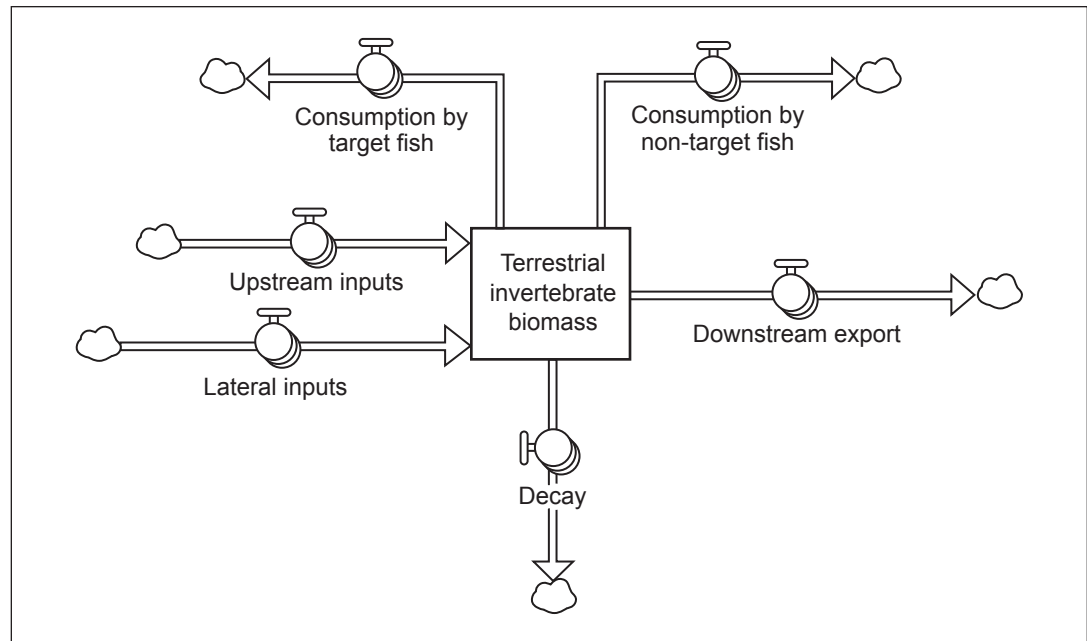


Figure 26—Stock and flow structure of the terrestrial invertebrate stock.

- **Terrestrial invertebrate decay:** Microbial decomposition of invertebrates is assumed to increase exponentially with water temperature.
- **Terrestrial invertebrate consumption:** Consumption represents the loss of invertebrate biomass to fish consumers. Consumption increases as the population of fish consumers increases and as the availability of invertebrates increases.
- **Terrestrial invertebrate downstream export and upstream inputs:** Downstream exports represent the loss of invertebrate biomass to downstream reaches resulting from hydraulic forces that scour the streambed and mobilize benthic material. Upstream inputs represent the terrestrial invertebrate biomass that is transported into the modeled reach from upstream.

4.1.5 Periphyton

The periphyton stock (P) represents instream primary producers: the community of algae, diatoms, bacteria, and fungi that grow on the streambed. Equation 5 in table 4 governs the dynamics of this stock. The stock and flow structure of the periphyton stock is shown in figure 27 and described below.

- **Periphyton primary production:** Periphyton production represents the growth of periphyton on the streambed and is a function of periphyton density (density dependence), water temperature, light availability (including sunlight and turbidity), stream nutrients, and water velocity. Apart

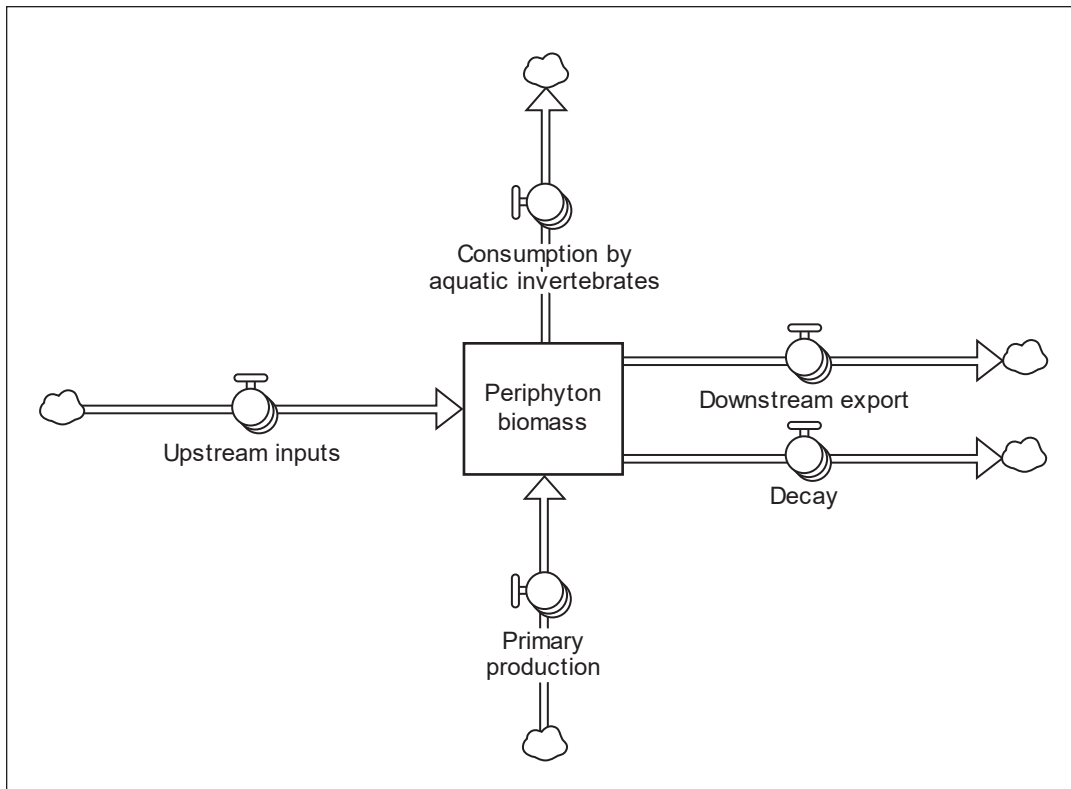


Figure 27—Stock and flow structure of the periphyton stock.

from density, which is controlled by an internal feedback loop (equation 10 in section 4.2.1, “Periphyton Production”), each of these factors can be manipulated from the Interface.

- **Periphyton consumption:** Consumption represents the loss of periphyton biomass to aquatic invertebrate consumption. Consumption increases as the population of invertebrate consumers increases and as the availability of periphyton increases. A small proportion of the periphyton biomass, the refuge biomass, is invulnerable to consumption and export.
- **Periphyton decay:** Microbial decomposition of periphyton is assumed to increase exponentially with water temperature.
- **Periphyton downstream export and upstream inputs:** Downstream exports represent the detachment and subsequent downstream transport of periphyton biomass owing to hydraulic forces that scour the streambed and mobilize benthic material. As with consumption, there is a refuge biomass of periphyton that is invulnerable to consumption and export. Upstream inputs represent the periphyton biomass that is exported from the upstream reach and transported into the modeled reach.

4.1.6 Terrestrial Detritus

The ATP model tracks both deciduous (D_d) and coniferous (D_c) detritus biomass within the terrestrial detritus stock (this is done using an “array” in Stella). The mass balance equation is the same for both types of detritus (generically represented as D_i in equation 6 in table 4). However, deciduous and coniferous detritus do have different parameter values associated with the timing, magnitude, and the quality (assimilation efficiency) of the leaf litter. Deciduous detritus is assumed to have a higher assimilation efficiency than coniferous detritus owing to the higher nutritional value of deciduous leaf litter (Hisabae et al. 2011, Richardson et al. 2005) (see also appendix). The stock and flow structure of the terrestrial detritus stock is shown in figure 28 and described below.

- Lateral inputs of detritus:** Leaf litter inputs enter the river reach from adjacent riparian vegetation. The magnitude and timing of these inputs are a function of the vegetation composition and coverage (Minshall and Rugenski 2006). It is assumed that the input of deciduous detritus to the

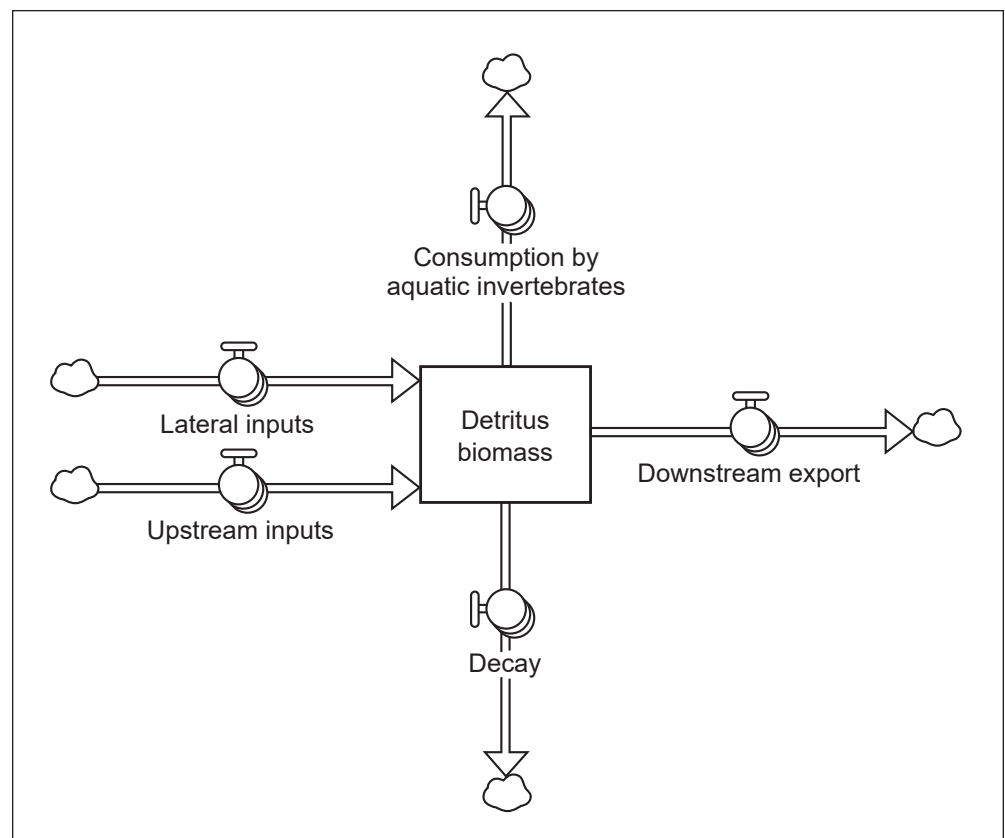


Figure 28—Stock and flow structure of the terrestrial detritus stock.

reach is normally distributed with the peak corresponding to fall leaf abscission, whereas coniferous leaf litter inputs are assumed to be uniformly distributed throughout the year.

- **Detritus consumption:** Consumption represents the loss of detritus biomass to aquatic invertebrate consumers. Consumption increases as the population of invertebrate consumers increases and as the availability of detritus increases.
- **Detritus decay:** Microbial decomposition of detritus is assumed to increase exponentially with water temperature. Coniferous detritus is assumed to decay at a slower rate than deciduous detritus owing to the characteristics of needles that limit microbial colonization and use (Richardson et al. 2005).
- **Detritus downstream export and upstream inputs:** Downstream exports represent the loss of detritus to downstream reaches resulting from hydraulic forces that scour the streambed. Upstream inputs represent the detritus biomass that is exported from the upstream reach and transported into the modeled reach.

4.1.7 Salmon Eggs

A proportion of the eggs from spawning salmon become available for consumption by fish. The salmon egg stock tracks this biomass of available eggs as it enters the stream food web. Equation 7 in table 4 governs the dynamics of this stock. The stock and flow structure of the salmon egg stock (E) is shown in figure 29 and described below.

- **Salmon egg biomass from spawning activities:** Salmon eggs become available for consumption when they are exposed by spillage (incomplete burial during deposition) (Moore and Schindler 2004) and superimposition of redds (i.e., salmon spawning on top of previously constructed redds) (Maunder 1997).
- **Salmon egg decay:** Microbial decomposition of salmon eggs is assumed to increase exponentially with water temperature.
- **Salmon egg consumption:** Consumption represents the loss of egg biomass to fish consumers. Consumption increases as the population of fish consumers increases and as the availability of eggs increases.
- **Salmon egg export and upstream input:** Downstream exports represent the loss of egg biomass to downstream reaches resulting from hydraulic forces that scour the streambed and mobilize benthic material. Upstream inputs represent the egg biomass that is transported into the modeled reach from upstream.

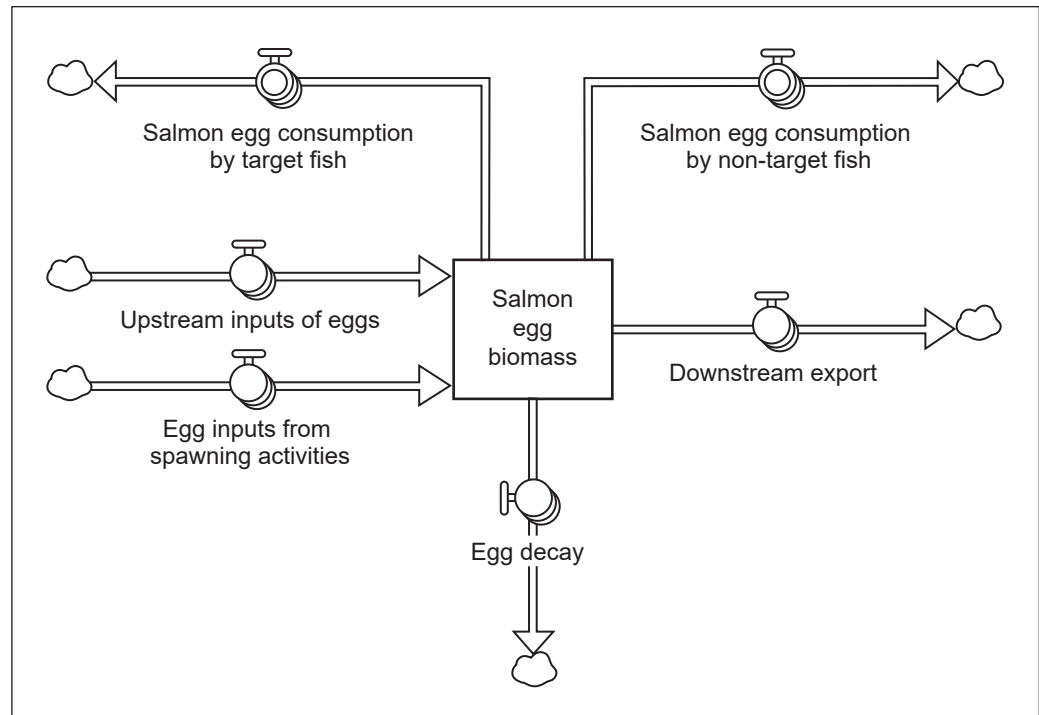


Figure 29—Stock and flow structure of the salmon egg stock.

4.1.8 Salmon Carcasses

After salmon spawners die, carcasses are deposited on the streambed and in adjacent terrestrial environments. When implemented, salmon carcass augmentation also contributes carcasses to these environments. Carcasses stranded in terrestrial habitats lead to an increase in terrestrial invertebrate inputs to the reach. Those carcasses that remain in the stream are subject to export, decay, and, after conditioning, consumption (equation 8 in table 4). The stock and flow structure of the conditioned salmon carcass stock (S) is shown in figure 30 and described below. The “unconditioned” salmon carcass biomass stock, also shown in figure 30, is subject to the same flows with exception of consumption.

- **Salmon carcass biomass input:** These inputs represent organic matter from the death of natural spawning salmon and salmon carcasses that are experimentally added to the stream, excluding the carcasses that are stranded in terrestrial habitats.
- **Salmon carcass consumption:** Aquatic invertebrates and both target and non-target fish consume conditioned salmon carcass material (Claeson et al. 2006). Conditioning occurs at a set rate (see appendix) and accounts for the physical and microbial decay processes that break carcasses into “bite size” pieces.

- **Salmon carcass decay:** Microbial decomposition of salmon carcasses is assumed to increase exponentially with water temperature.
- **Salmon carcass downstream export and upstream inputs:** Downstream exports represent the loss of carcasses to downstream reaches as a result of hydraulic forces that scour the streambed. Upstream inputs represent the input of carcass biomass that is exported from the upstream reach into the modeled reach.

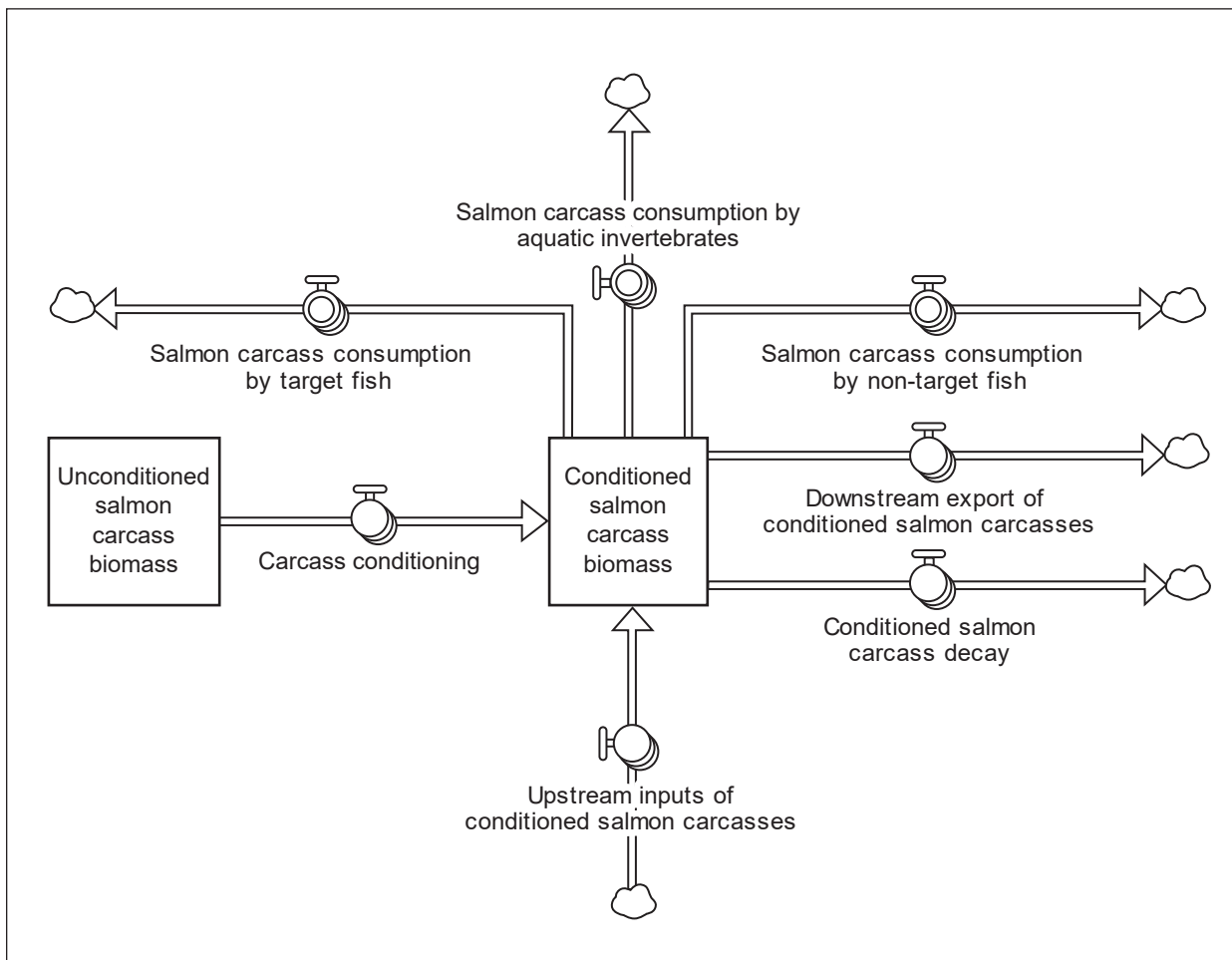


Figure 30—Stock and flow structure of the conditioned salmon carcass stock. The unconditioned salmon carcass stock is subject to the same flows (although not shown here) as the conditioned stock with the exception of consumption.

4.2 Inflows and Outflows

The following flows, shown as terms in table 4, contribute to the biomass gains and losses for the stocks. Here we describe the functional form of these flows and how they relate to the environmental conditions of the reach and adjacent riparian zone.

4.2.1 Periphyton Production

Periphyton production (g AFDM/day) is the process by which periphyton biomass ($Biomass_p$; g AFDM) is accrued on the streambed. The production formulation is adapted from Bellmore et al. (2014):

$$Production = Biomass_p \times Growth_{max} \times f_1(Temp) \times f_2(Density) \times f_3(Light) \times f_4(Nutrients) \times f_5(Velocity)$$

where $Growth_{max}$ is the maximum daily growth rate (g AFDM/g AFDM/day) when there is no density dependence, resources are not limiting, and environmental conditions are ideal. The maximum growth rate is multiplied by five dimensionless functions that account for the limiting effects of water temperature (f_1), biomass density (f_2), light (f_3), nutrients (f_4), and water velocity (f_5). The functions range from 0 to 1, where a value of 1 indicates that the factor is non-limiting and a value of 0 means the factor is so limiting that production is halted.

The temperature function $f_1(Temp)$ limits the rate of production when water temperatures are above or below the optimum temperature. The function is represented by an asymmetrical Gaussian distribution (Rutherford et al. 2000), in which production decreases more sharply when temperatures exceed the optimum compared to when temperatures are below the optimum. The temperature limitation function for biomass stock i has the form:

$$f_1 = \exp \left(- \left(\frac{Temp - Temp_{opt,i}}{(Temp_{opt,i} - Temp_{min,i}) / \sqrt{\ln(100)}} \right)^2 \right), \text{ if } Temp < Temp_{opt,i}$$

$$f_1 = \exp \left(- \left(\frac{Temp - Temp_{opt,i}}{(Temp_{max,i} - Temp_{opt,i}) / \sqrt{\ln(100)}} \right)^2 \right), \text{ if } Temp \geq Temp_{opt,i}$$
(9)

where i is the biomass stock in question, $Temp_{opt,i}$ is the optimum temperature (°C) for production, and $Temp_{min,i}$ and $Temp_{max,i}$ are the minimum and maximum threshold temperatures, respectively, at which production is 1 percent of what can be achieved at the optimum temperature.

The remaining functions are represented by Michaelis-Menten functions, in which the effect of each factor on periphyton growth follows a type II functional

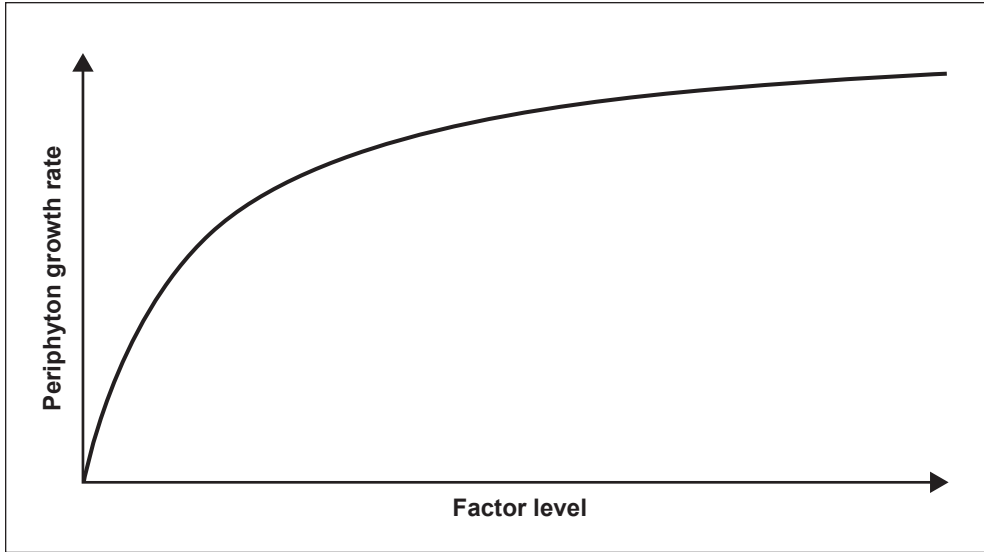


Figure 31—Example of type II functional response for factors affecting periphyton growth.

response (Gotelli 2001) (fig. 31). With this functional response, the growth rate increases linearly at low levels of the factor (e.g., low biomass densities) and then at higher factor levels, the rate gradually plateaus to a maximum value.

The density limitation function, $f_2(Density)$, accounts for self-limitation owing to competition for light and nutrients (Hill and Harvey 1990, Rutherford et al. 2000). It has the form (McIntire 1973):

$$f_2 = 1 - \frac{\frac{Biomass_i}{Area}}{\left(\frac{Biomass_i}{Area}\right) + (1 - p_{scour})k_i} \quad (10)$$

where $Area$ is the wetted area of the reach (m^2) and k_i is the half-saturation value or the biomass per square meter at which the growth rate is half the maximum. The half-saturation value is multiplied by the proportion of the streambed not being scoured at that time step ($1 - p_{scour}$), as actively scoured surfaces do not support periphyton growth).

The limiting effect of light $f_3 (Light)$ on production is modeled as:

$$f_3 = \frac{PAR_{bed}}{PAR_{bed} + k_{par}}$$

where PAR_{bed} is the amount of sunlight or photosynthetically active radiation (PAR; $mol/m^2/day$) that reaches the streambed, and k_{par} is the half-saturation level for PAR. Sunlight at the streambed is modeled following Julian et al. (2008) (fig. 32):

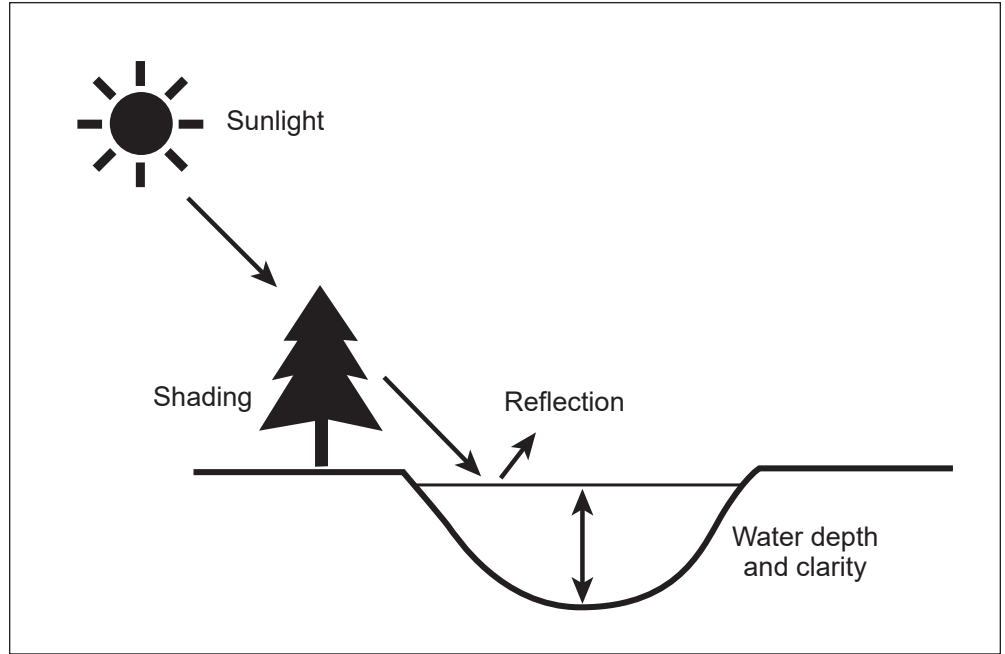


Figure 32—Conceptual diagram of factors affecting streambed light availability (adapted from Julian et al. 2008). Before reaching the streambed, the amount of above canopy PAR (sunlight) is reduced by shading, reflection off the water, and increasing water depth and turbidity (clarity). PAR = photosynthetically active radiation.

$$PAR_{bed} = (PAR_{can} \times Solar\ access \times P_{reflect})e^{-0.17 \times NT \times Depth}$$

where PAR_{can} is the above canopy PAR, *Solar access* is the proportion of sunlight that reaches the surface of the water after shading by topography or riparian vegetation (i.e., 1.0-proportion of the stream shaded), $P_{reflect}$ is the proportion of PAR that enters the water after reflection, NT is turbidity in nephelometric turbidity units (NTUs), and $Depth$ is the water depth (m). The value of 0.17 is the turbidity coefficient for light attenuation that describes the strength of the relationship between turbidity and light attenuation (Julian et al. 2008).

The effect of nutrient limitation on production is represented by the function f_4 *nutrients*. Only the most limiting nutrient (minimum value) of either dissolved inorganic nitrogen (DIN; $NO_2 + NO_3 + NH_4$) or soluble reactive phosphorus (SRP) affects the growth rate at a given time step. The nutrient limitation function has the structure:

$$f_4 = \text{MIN} \left(\frac{[DIN]}{[DIN] + k_{DIN}}, \frac{[SRP]}{[SRP] + k_{SRP}} \right) \quad (9)$$

where $[DIN]$ and $[SRP]$ are the concentrations (mg/L) of nitrogen and phosphorus in the water column, and k_{DIN} and k_{SRP} are the half saturation levels of the nutrients.

Finally, low water velocities (*Velocity*; m/s) can also limit nutrient uptake and export of metabolic waste. The water velocity limitation function f_5 (*Velocity*) has the form (McIntire 1973):

$$f_5 = \text{MIN} \left(1, 0.2 + \frac{\text{Velocity}}{\text{Velocity} + k_v} \right)$$

where k_v is half saturation level for water velocity.

4.2.2 Consumption

Consumption represents the amount of prey *X* biomass ingested by predator *Y* and is modeled as (Bellmore et al. 2017):

$$\text{Consumption}_{XY} = \text{Biomass}_Y \times \text{Consumption rate}_{XY}$$

where Biomass_Y is the predator biomass (g AFDM/day) and $\text{Consumption rate}_{XY}$ is the rate at which predator *Y* consumes prey *X* (g AFDM/g AFDM/day). The consumption rate is modeled as:

$$\text{Consumption rate}_{XY} = \text{Consumption}_{\max,Y} \times f_1(\text{Temp}) \times f_6(\text{PreyAvailability}, \text{SelfLimit}) \times \text{Selection}_{XY}$$

where $\text{Consumption}_{\max,Y}$ is the maximum rate of consumption by predator *Y* when temperatures are optimal, there is no density dependence, and prey resources are not limiting. Functions f_1 and f_6 describe the limiting effects of water temperature (f_1) and prey availability and predator self-limitation (f_6). They range from 0 to 1, where a value of 1 indicates the factor is nonlimiting, and with a value of 0, the factor is so severely limiting that consumption is halted. The proportion of predator *Y* consumption directed at prey *X* is represented by Selection_{XY} .

The temperature function, $f_1(\text{Temp})$, is the same function used in the production calculation (equation 9, section 4.2.1, “Periphyton Production”) and limits consumption when water temperatures are above or below the optimum temperature.

The limiting effect of prey availability and predator density (f_6) is described by a type II functional response (Gotelli 2001):

$$f_6 = \frac{\sum_i^n \text{Biomass}_i - \text{Biomass}_i^*}{\sum_i^n (\text{Biomass}_i - \text{Biomass}_i^*) + (k_Y + \gamma_Y \times \text{Biomass density}_{XY})}$$

where Biomass_i is the biomass (g AFDM/day) of prey type *i*, Biomass_i^* is the biomass (g AFDM/day) of prey type *i* that is unavailable to consumers (i.e., refuge biomass of periphyton), and *n* is the total number of prey types available to predator *Y*. In the denominator, k_Y is the density-independent prey biomass half saturation

level, and γ_Y is a dimensionless self-interaction parameter ($\gamma_Y > 0$ for interference, $\gamma_Y < 0$ for facilitation) that adjusts consumption rates for consumer biomass density (*Biomass density*_Y; g AFDM/m²/day).

In the model, consumers maximize energy intake by adjusting foraging to preferentially select prey items that are highly abundant and/or of high quality. The proportion of predator *Y* consumption directed at prey *X* is calculated as follows:

$$Selection_{XY} = \frac{\alpha_{XY}(Biomass_X - Biomass_X^*)}{\sum_i \alpha_{iY}(Biomass_i - Biomass_i^*)}$$

With this formulation, the consumption rate of prey *X* by predator *Y* is the product of the quantity (available biomass) and quality (assimilation efficiency; α_{XY}) of prey *X*, relative to the summation of the quantity and quality of each prey type *i* available to the predator. This predator-switching mechanism releases prey from strong predation when prey densities become low (sensu Holling type III functional response) (Gotelli 2001).

The biomass gains of predator *Y* resulting from consumption of prey *X* are the product of the consumed biomass and the quality of the prey. In the model, these gains are summed across consumed prey types (*n*) to give the organic matter assimilation flow (e.g., see fig. 23):

$$Organic\ matter\ assimilation_Y = \sum_i^n Consumption_{iY} \times \alpha_{iY}$$

4.2.3 Export

Export represents the downstream transport of stock biomass (*Biomass*_i; g AFDM/day) from the modeled reach. Biomass may be exported as a result of streambed scour (combined impact of hydraulic forces and bioturbation) or the effect of friction velocity on the streambed.

$$Export_i = \left(\frac{Biomass_i - Biomass_i^*}{Reach\ length} \right) \times (r_{scour} + r_{friction\ velocity,i} \times (1 - r_{scour})) \quad (12)$$

where *Biomass*_i^{*} is a refuge biomass that is not susceptible to mobilization or consumption (e.g., hyporheic invertebrates; g AFDM/day), *Reach length* is the length of the modeled reach (m), and r_{scour} and $r_{friction\ velocity,i}$ represent the rates (g AFDM/g AFDM/day) of biomass loss to benthic substrate mobilization (scour) and friction velocity on the streambed, respectively. The refuge biomass is calculated as a refuge biomass per square meter multiplied by the wetted area (m²) of the modeled reach when streamflow is minimized.

Export resulting from scouring of the streambed (r_{scour}) is the proportion of the streambed that is newly mobilized by streamflows at each time step (Bellmore et al. 2014). The rate of export from scouring for biomass stock i is calculated as:

$$r_{scour} = \begin{cases} \frac{(1 - p_{scour,time}) - (1 - p_{scour,time-1})}{(1 - p_{scour,time-1})} & \text{if } p_{scour,time} > p_{scour,time-1} \\ 0 & \text{else} \end{cases}$$

where $p_{scour,time}$ is the proportion of streambed that is exported at a given time step. This formulation allows for a positive rate of scour only when the proportion of the streambed scour increases from one time step to the next. When the proportion of streambed scour stabilizes (or decreases), no additional biomass is removed from the reach by scour.

The proportion of the streambed that is not mobilized by scour ($1 - r_{scour}$) is subject to export because of friction velocity on the streambed. The rate of export resulting from friction velocity is calculated using a sigmoid function specific to biomass stock i (Otto and Day 2007):

$$r_{friction\ velocity,i} = \left(\frac{0.01e^{a_i \times friction\ velocity}}{0.01e^{a_i \times friction\ velocity} + 0.99} - 0.01 \right)$$

where a_i is a parameter that determines the sharpness at which the sigmoid curve approaches its maximum of 0.99 (i.e., 99 percent biomass export, named “slope of S shaped function” in the model). See section 4.2.10, “Physical Controls,” for a description of how friction velocity and the proportion of streambed scoured are calculated.

4.2.4 Respiration and Decay

Respiration represents the loss of stock biomass ($Biomass_i$; g AFDM/day) resulting from the metabolic requirements of aquatic invertebrates and fish, whereas decay represents the loss of periphyton, terrestrial detritus, and salmon egg and carcass biomass to microbial decay. The rates of respiration and decay increase exponentially with increasing water temperature as follows (Rutherford et al. 2000):

$$Respiration_i = Biomass_i \times Respiration\ rate_{ref,i} \times \Theta_i^{Temp - Temp_{ref}}$$

$$Decay_i = Biomass_i \times Decay\ rate_{ref,i} \times \Theta_i^{Temp - Temp_{ref}}$$

where $Respiration\ rate_{ref,i}$ and $Decay\ rate_{ref,i}$ are the respiration and decay rates (g AFDM/g AFDM/day), respectively, at the reference temperature ($Temp_{ref} = 20\ ^\circ\text{C}$ for all food web members except for fish, for which $Temp_{ref} = 25\ ^\circ\text{C}$) and Θ_i is a dimensionless temperature coefficient that describes the shape of the exponential relationship between temperature and the respiration or decay rate.

4.2.5 Mortality

Mortality is an additional loss term for fish and aquatic invertebrates ($Biomass_i$; g AFDM/day) and is controlled by a constant mortality rate ($Mortality\ rate_i$; g AFDM/g AFDM/day).

$$Mortality_i = Biomass_i \times Mortality\ rate_i$$

4.2.6 Lateral Inputs

Adjacent riparian vegetation contributes leaf-litter and terrestrial invertebrates to the stream. These are termed lateral inputs in the model ($Lateral_i$). The magnitude and timing of the detrital leaf-litter inputs are a function of riparian vegetation composition and coverage (Minshall and Rugenski 2006). We assume that the input of deciduous detritus to the reach is normally distributed with the peak corresponding to autumn leaf abscission, whereas coniferous leaf-litter inputs are uniformly distributed throughout the year. Lateral detrital inputs (g AFDM/day) are calculated as:

$$Lateral_{D_i} = Input_{D_i} \times p_{covered} \times p_{veg\ type_i}$$

where i is either d , deciduous, or c , coniferous, $Input_{D_i}$ is the daily input (g AFDM/day) of terrestrial detritus to the stream per square meter of vegetation, $p_{covered}$ is the proportion of the stream covered by vegetation, and $p_{veg\ type_i}$ is the proportion of the riparian vegetation that is deciduous vs coniferous. The daily input of leaf litter is an exogenous input to the model that is calculated in the associated import spreadsheet.

Lateral inputs of terrestrial invertebrates also are an exogenous input to the model. The magnitude and timing of the inputs are calculated similarly to lateral inputs of terrestrial detritus. The daily input of terrestrial invertebrates per square meter of wetted area is modeled as:

$$Lateral_T = Input_T \times p_{covered} \times Carcass\ Stranding\ Multiplier$$

where $Input_T$ is the daily terrestrial invertebrate input (g AFDM/day) to the stream per square meter of vegetation. Daily values of $Input_T$ are imported from the import spreadsheet and are calculated based on a normal distribution around the peak time of terrestrial invertebrate input (user specified). The *Carcass Stranding Multiplier* adjusts the terrestrial invertebrate input for the increase associated with salmon carcasses stranded in terrestrial habitats, such as gravel bars. This multiplier assumes that carcasses stranded in terrestrial habitats attract invertebrates to the stream-side, which increases the lateral flux invertebrates into the stream. This multiplier is as a type II functional response with the form:

$$\text{Carcass Stranding Multiplier} = \frac{(MAX_{stranding} - 1)(Biomass_{stranded})}{Biomass_{stranded} + k_{stranded}} + 1$$

where $MAX_{stranding}$ is the maximum possible effect of salmon carcasses stranded in terrestrial habitats on terrestrial invertebrate inputs, $Biomass_{stranded}$ is the biomass of salmon carcasses stranded in terrestrial habitats (g AFDM; including both returning salmon carcasses and experimentally added carcasses), and $k_{stranded}$ is the half saturation level or the biomass of stranded carcasses at which the terrestrial invertebrate response is half of the maximum. Carcasses stranded in terrestrial habitats are assumed to remain for 45 days, at which point they no longer affect terrestrial invertebrate biomass. When salmon carcasses are absent, the multiplier takes a value of 1.0, and therefore, does not influence the terrestrial invertebrate inputs.

4.2.7 Upstream Inputs

Upstream inputs $Upstream_i$ (g AFDM/day) represent the biomass of the stock i that is transported into the modeled river reach via export from upstream reaches. To represent this process, an “upstream” reach is included in the model (see section 1.6, “How the ATP Model Runs”).

4.2.8 Marine-Derived Biomass Inputs

Marine-derived biomass inputs ($Marine_S$, $Marine_E$; g AFDM/day) represent a biomass gain to the stocks of carcasses and eggs from returning salmon and added salmon carcasses. The magnitude of the carcass input is proportional to the number of returning adult salmon/added salmon carcasses and their average mass (see section 4.2.9, “Returning Salmon Spawners”):

$$Marine_S = (Salmon_{wetmass} \times \#_{salmon} \times 0.2)(1 - p_{strand})$$

where $Marine_S$ is the salmon carcass biomass from returning salmon and added salmon carcasses, $Salmon_{wetmass}$ is the mass of returning and added salmon in grams wet mass, $\#_{salmon}$ is the number of returning or added salmon, 0.2 is the conversion factor for salmon wet mass to AFDM (Elliott 1976), and p_{strand} is the proportion of carcass biomass that is stranded in terrestrial habitats.

$Marine_E$ represents the salmon eggs from spawning salmon that become available for consumption when they are exposed by spillage (incomplete burial during deposition) (Moore and Schindler 2004) and superimposition of redds (see section 4.2.9.2, “Redd superimposition, streambed scour, and salmon egg availability”).

4.2.9 Returning Salmon Spawners

The ATP model tracks salmon through four stages: (1) arrival of salmon in the modeled reach, (2) spawning, (3) post-spawn salmon, and (4) mortality and decomposition. The arrival of salmon is assumed to be normally distributed around an average arrival time (see section 2.3.2.1, “Detailed parameter descriptions”), after which salmon remain in the modeled river reach for a specified number of days prior to spawning. Once spawning commences, females are assumed to be continuously involved in redd building activities for a set number of days (see appendix). Post-spawn salmon remain in the modeled river reach until death. Following death, a proportion of carcasses become stranded in terrestrial habitats. Those that remain in the stream are available for consumption by invertebrates and fish (see section 4.2.8, “Marine-Derived Biomass Inputs”).

4.2.9.1 Nutrient contributions from salmon—

Salmon contribute nutrients to the stream through excretion while alive and through the leaching of nutrients from carcasses following death. The contribution of dissolved inorganic nitrogen (DIN; $\text{NO}_3 + \text{NO}_2 + \text{NH}_3$) and soluble reactive phosphorus (SRP) from live salmon and carcasses is added to background nutrient concentrations (mg/L) to calculate the nutrient availability for periphyton growth (equation 11, section 4.2.1, “Periphyton Production”). Nutrient excretions from live salmon are calculated as (Bellmore et al. 2014):

$$[\text{DIN}_{\text{salmon}}] = \frac{\text{Biomass}_{\text{live}} \times \text{DIN}_{\text{excret}}}{\text{Discharge} \times 86,400}$$

$$[\text{SRP}_{\text{salmon}}] = \frac{\text{Biomass}_{\text{live}} \times \text{SRP}_{\text{excret}}}{\text{Discharge} \times 86,400}$$

where $\text{Biomass}_{\text{live}}$ is the biomass of live salmon (g wet mass/day) at the spawning ground (number of live salmon multiplied by the average salmon wet mass), $\text{DIN}_{\text{excret}}$ and $\text{SRP}_{\text{excret}}$ are nutrient excretion rates (mg of nutrients/g wet mass of salmon/day), and Discharge is the stream discharge (L/s). The discharge is multiplied by 86,400 seconds per day, to give the total volume of water moving through the reach per day.

After death, we assume that nutrients leach from the carcasses at a rate of one-tenth of the excretion rate from live salmon:

$$[\text{DIN}_{\text{carcass}}] = \frac{\left(\frac{\text{Biomass}_s}{0.2}\right) \text{DIN}_{\text{leach}}}{\text{Discharge} \times 86,400}$$

$$[\text{SRP}_{\text{salmon}}] = \frac{\left(\frac{\text{Biomass}_s}{0.2}\right) \text{SRP}_{\text{leach}}}{\text{Discharge} \times 86,400}$$

where $Biomass_S$ is the salmon carcass biomass (g AFDM/day). The carcass biomass in grams AFDM is converted to wet mass by dividing by 0.2, which is the wet mass to AFDM conversion for salmon (Elliott 1976). DIN_{leach} and SRP_{leach} (mg of nutrients/g wet mass of salmon/day) are the nutrient leaching rates.

4.2.9.2 Redd superimposition, streambed scour, and salmon egg availability—

During redd construction, salmon can disturb the benthic habitat and subsequently detach and mobilize periphyton, detritus, and aquatic invertebrates (Janetski et al. 2009). We assume that habitat disturbance occurs continuously during spawning activities. The proportion of the streambed disturbed by spawning ($p_{disturb}$) is a function of the area excavated by salmon and the wetted area of the modeled reach (Bellmore et al. 2014):

$$p_{disturb} = \frac{Redds_{const} \times Area_{redd}}{Area}$$

where $Redds_{const}$ is the number of redd sites constructed in open habitat, $Area_{redd}$ is the average redd area (m²), and $Area$ is the wetted area of the modeled reach (m²). The proportion of the streambed disturbed by spawning salmon is added to the proportion of the bed scoured by hydraulic forces (p_{scour}) and is used to calculate the export rates of periphyton, detritus, and aquatic invertebrates (equation 12).

In contrast to $Redds_{const}$, the number of redds successfully constructed in open habitat ($Redds_{success}$) accounts for redd superimposition, which occurs in the model when redds overlap because of limitations in suitable spawning habitat and the number of spawning salmon. It is given by the function (Maunder 1997):

$$Redds_{success} = K_{redd} \left(1 - \exp \left(-\frac{Spawn_{female}}{K_{redd}} \right) \right)$$

where K_{redd} is the redd carrying capacity of the river reach and $Spawn_{female}$ is the number of female salmon spawners. K_{redd} is calculated as the suitable spawning habitat ($Area_{suitable}$, m²) divided by the average redd area. $Area_{suitable}$ is the proportion of the modeled reach with suitably sized substrate for spawning (1 to 15 cm in diameter) (Quinn 2005) that is not actively being scoured by hydraulic forces at the time of spawning. The ATP model does not account for scouring of redds by high flows.

The number of redds superimposed ($Redds_{super}$) is given by:

$$Redds_{super} = Spawn_{female} - Redds_{success}$$

Redd superimposition makes salmon eggs available for consumers. Additionally, salmon eggs become available because of egg spillage (incomplete burial during deposition) (Moore and Schindler 2004). Salmon egg availability is calculated as:

$$Marine_E = (Redds_{super} + (p_{spill} \times Redds_{const}))(Egg_{mass} \times Fecundity)$$

where $Marine_E$ is the salmon egg biomass input (g AFDM/day), p_{spill} is the proportion of egg spillage, Egg_{mass} is the mass of a salmon egg (g AFDM/egg), and $Fecundity$ is the fecundity of a spawning female salmon (eggs/female).

4.2.10 Physical Controls

In the ATP model, food web dynamics are linked to the physical and hydraulic conditions of the reach. Total discharge is a user input that the model divides between the main and side channel based on whether the side channel is turned on and on the proportion of flow in the side channel. Hydraulic curves are then used to look up the average wetted width and water depth at a given discharge. The model uses graphical functions (see section 2.2, “Navigating the Model Interface,” for directions on use) to express the hydraulic curves, which are one-dimensional rating curves that describe the relationship between discharge and the reach averaged water depth and wetted width. The one-dimensional rating curves can be created by summarizing the output of a two-dimensional hydraulic model run at a range of discharges that reflect the annual hydrograph of the modeled reach (section 3.1.1.1, “Hydraulic model information”).

The widths and depths from the graphical functions are used to calculate the water velocity using the continuity equation (Gordon et al. 2004). In turn, friction velocity (m/s) is calculated from the channel slope ($Slope$, m/m), hydraulic radius ($Hydraulic\ radius$, m), and acceleration due to gravity (9.81 , m/s²).

$$Friction\ velocity = \sqrt{9.81 \times Slope \times Hydraulic\ radius}$$

Friction velocity is used to calculate the export rate of organic matter from the modeled reach.

The proportion of streambed actively being scoured at a given time step (p_{scour}) is also used in export rate calculations. It is evaluated by first determining the diameter of substrate at the threshold of motion ($Critical\ substrate\ size$, m) for a given channel slope and hydraulic radius (Gordon et al. 2004):

$$Critical\ substrate\ size = \frac{Hydraulic\ radius \times Slope}{(\rho_s - 1) \times \tau^*}$$

where ρ_s is substrate density (2.65 kg/m^3) (Gordon et al. 2004) and τ^* is the Shields number (0.045) following Henderson (1966: 415). Then, the calculated critical substrate size is compared to the cumulative substrate size distribution at each time step to determine the proportion of the streambed containing substrates smaller than the critical size; this represents the proportion of the streambed actively scoured (p_{scour}) by hydraulic forces.

Similarly, the graphical function for the proportion of wetted area suitable for fish relates discharge to the proportion of suitable area. It is based on habitat suitability indices and represents the average proportion of the reach with water depths and velocities preferred by the species in question (juvenile Chinook salmon for the built-in model example) (Raleigh et al. 1986) for a given discharge. The proportion of wetted area suitable affects the biomass density of target fish.

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U.S. Equivalents

When you know:	Multiply by:	To find:
Centimeters (cm)	0.394	Inches
Meters (m)	3.28	Feet
Square meters (m ²)	10.76	Square feet
Cubic meters (m ³)	35.3	Cubic feet
Cubic meters per second (m ³ /s)	35.3	Cubic feet per second
Liters (L)	0.0353	Cubic feet
Liters	0.265	Gallons
Milligrams (mg)	2.2×10^{-6}	Pounds
Grams (g)	0.0352	Ounces
Grams	0.0022	Pounds
Degrees Celsius (°C)	1.8 °C + 32	Degrees Fahrenheit

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Appendix: Model parameters (i.e., parameters not specific to the modeled reach) used in the Aquatic Trophic Productivity model

Module	Parameter	Description	Units ^a	Value	Sources
Target fish (F)	α_{AF}	Proportion of ingested aquatic invertebrate biomass that is assimilated	Grams/gram	0.75	Cross et al. 2011
	α_{TF}	Proportion of ingested terrestrial invertebrate biomass that is assimilated	Grams/gram	0.70	Cross et al. 2011
	α_{CF}	Proportion of ingested added salmon carcass biomass that is assimilated	Grams/gram	0.90	Assumed
	α_{EF}	Proportion of ingested salmon egg biomass that is assimilated	Grams/gram	0.95	Assumed
	$\text{Consumption}_{\max,F}$	Maximum rate of consumption at optimum temperature	Grams/gram/day	0.16	Hanson et al. 1997
	$\text{Temp}_{\text{opt},F}$	Optimum temperature for consumption	°C	16.0	Hanson et al. 1997
	$\text{Temp}_{\max,F}$	Maximum temperature for consumption	°C	25.0	Hanson et al. 1997
	$\text{Temp}_{\min,F}$	Minimum temperature for consumption	°C	-5.0	Hanson et al. 1997
	γ_F	Dimensionless self-interaction parameter	Unitless	3.0	Assumed
	k_F	Prey biomass half saturation level	Grams/square meter/day	2.0	Assumed
	Respiration	Rate of respiration at 25 °C	Grams/gram/day	0.026	Hanson et al. 1997
	ref,F	Temperature coefficient describing shape of exponential relationship between temperature and respiration rate	Unitless	1.07	Hanson et al. 1997
	θ_F				
	Mortality _F	Daily mortality rate	Grams/gram/day	0.005	Assumed
Non-target fish (N)	α_{FN}	Proportion of ingested fish biomass that is assimilated	Grams/gram	0.90	Cross et al. 2011
	α_{AN}	Proportion of ingested aquatic invertebrate biomass that is assimilated	Grams/gram	0.75	Cross et al. 2011
	α_{TN}	Proportion of ingested terrestrial invertebrate biomass that is assimilated	Grams/gram	0.70	Cross et al. 2011
	α_{CN}	Proportion of ingested added salmon carcass biomass that is assimilated	Grams/gram	0.90	Assumed

Module	Parameter	Description	Units ^a	Value	Sources
Aquatic invertebrates (A)	α_{EN}	Proportion of ingested salmon egg biomass that is assimilated	Grams/gram	0.95	Assumed
	$Consumption_{max,N}$	Maximum rate of consumption when temperature is optimum	Grams/gram/day	0.16	Hanson et al. 1997
	$Temp_{opt,N}$	Optimum temperature for consumption	°C	16.0	Hanson et al. 1997
	$Temp_{max,N}$	Maximum temperature for consumption	°C	25.0	Hanson et al. 1997
	$Temp_{min,N}$	Minimum temperature for consumption	°C	-5.0	Hanson et al. 1997
	γ_N	Dimensionless predatory fish self-interaction scaling parameter	Unitless	12.0	Assumed
	k_N	Prey half saturation for predatory fish that experiences no conspecific influence on its intake	Grams/square meter/day	2.0	Assumed
	Respiration _{ref,N}	Rate of respiration at 25 °C	Grams/gram/day	0.026	Hanson et al. 1997
	θ_N	Temperature coefficient describing shape of exponential relationship between temperature and respiration rate	Unitless	1.07	Hanson et al. 1997
	Mortality _N	Daily mortality rate	Grams/gram/day	0.005	Assumed
	α_{pA}	Proportion of ingested periphyton biomass that is assimilated	Grams/gram	0.40	Cross et al. 2011, McCullough et al. 1979, McIntire 1996, Rutherford et al. 2000
	$\alpha_{D_d^A}$	Proportion of ingested deciduous detritus biomass that is assimilated	Grams/gram	0.20	Cross et al. 2011, Grafius and Anderson 1979, McIntire 1996
	$\alpha_{D_c^A}$	Proportion of ingested coniferous detritus biomass that is assimilated	Grams/gram	0.05	Assumed
	α_{S_A}	Proportion of ingested returning salmon carcass biomass that is assimilated	Grams/gram	0.70	Cross et al. 2011
	α_{C_A}	Proportion of ingested added salmon carcass biomass that is assimilated	Grams/gram	0.70	Cross et al. 2011
	$Consumption_{max,A}$	Maximum rate of consumption when temperature is optimum	Grams/gram/day	0.5	D'Angelo et al. 1997, Grafius and Anderson 1979, McIntire 1996, Rutherford et al. 2000

Module	Parameter	Description	Units ^a	Value	Sources
Terrestrial invertebrates (T)	Temp _{opt,A}	Optimum temperature for consumption	°C	15.0	McIntire 1996, Rutherford et al. 2000
	Temp _{max,A}	Maximum temperature for consumption	°C	26.0	Quinn et al. 1994
	Temp _{min,A}	Minimum temperature for consumption	°C	-10.0	Assumed
	γ_A	Dimensionless self-interaction parameter	Unitless	9.0	Assumed
	k _A	Prey biomass half saturation level	Grams/square meter/day	2.0	Assumed
	Respiration _{ref,A}	Rate of respiration at 20 °C	Grams/gram/day	0.05	D'Angelo et al. 1997, McIntire 1996, Rutherford et al. 2000
	Mortality _A	Daily mortality rate	Grams/gram/day	0.017	Assumed
	θ_4	Temperature coefficient describing shape of exponential relationship between temperature and respiration rate	Unitless	1.05	Rutherford et al. 2000
	α_A	Shape parameter for export rate equation	Unitless	7.0	Assumed
	Biomass _A [*]	Refuge biomass that is invulnerable to predation and export	Grams/square meter/day	0.05	Assumed
	Decay _{ref,T}	Terrestrial invertebrate rate of decay at 20 °C	Grams/gram/day	0.035	Assumed
	θ_T	Temperature coefficient describing shape of exponential relationship between temperature and decay rate	Unitless	1.08	Abelho 2001, Martinez et al. 2014
	α_T	Shape parameter for export rate equation	Unitless	18.0	Assumed
	—	Maximum increase of invertebrates resulting from salmon carcass stranding	Unitless	3.0	Assumed
Periphyton (P)	—	Half saturation level of stranded salmon carcasses	Grams/square meter/day	0.2	Assumed
	Growth _{max,P}	Maximum rate of growth when temperature is optimum	Grams/gram/day	1.1	Boulêtreau et al. 2006, Fovet et al. 2010, Schuwirth et al. 2011
	Temp _{opt,P}	Optimum temperature for growth	°C	25.0	Butterwick et al. 2005, DeNicola 1990, Rutherford et al. 2000

Module	Parameter	Description	Units ^a	Value	Sources
Terrestrial detritus (D _c and D _d)	Temp _{max,P}	Maximum temperature for growth	°C	30.0	Butterwick et al. 2005, DeNicola 1990, Rutherford et al. 2000
	Temp _{min,P}	Minimum temperature for growth	°C	-19.0	Butterwick et al. 2005, DeNicola 1990, Rutherford et al. 2000
	k _P	Density half saturation for growth	Grams/square meter/day	4.0	Boulétreau et al. 2006, McIntire 1973, Rutherford et al. 2000, Schuwirth et al. 2011
	k _{par}	PAR half-saturation level	Moles/square meter/day	5.0	Hill et al. 2009, Uehlinger et al. 1996
	k _{DIN}	Dissolved inorganic nitrogen (DIN) half-saturation level	Milligrams/liter/day	0.02	Chapra 1997, Jørgensen et al. 1991, Rutherford et al. 2000
	k _{SRP}	Soluble reactive phosphorus (SRP) half-saturation level	Milligrams/liter/day	0.005	Chapra 1997, Jørgensen et al. 1991, Rutherford et al. 2000
	k _v	Water velocity half-saturation level	Meters/second/day	0.18	McIntire 1973, 1996
	Decay _{ref,P}	Periphyton rate of decay at 20 °C	Grams/gram/day	0.035	Hamilton and Schladow 1997, Rutherford et al. 2000
	θ _P	Temperature coefficient describing shape of exponential relationship between temperature and decay rate	Unitless	1.08	Abdul-Aziz et al. 2010, Chapra 1997
	α _P	Shape parameter for export rate equation	Unitless	10.0	Assumed
	Biomass _P *	Refuge biomass that is invulnerable to predation and export	Grams/square meter/day	0.5	Assumed
	Decay _{ref,D_d}	Deciduous detritus rate of decay at 20 °C	Grams/gram/day	0.015	Abelho 2001, Martínez et al. 2014, Richardson et al. 2004, Webster et al. 2001
	Decay _{ref,D_c}	Coniferous detritus rate of decay at 20 °C	Grams/gram/day	0.009	Assumed to be 60 percent of deciduous rate. (Richardson et al. 2004, Webster et al. 2001)

Module	Parameter	Description	Units ^a	Value	Sources
Returning salmon carcasses, S	θ_{Di}	Temperature coefficient describing shape of exponential relationship between temperature and decay rate	Unitless	1.08	Abelho 2001, Martínez et al. 2014
	α_{Di}	Shape parameter for export rate equation	Unitless	18.0	Assumed
	$\text{Decay}_{\text{ref},S}$	Rate of salmon carcass decay at 20 °C	Grams/gram/day	0.15	Chaloner et al. 2002, Chidami and Amyot 2008, Fenoglio et al. 2005, Minshall et al. 1991, Rüegg et al. 2014, Weaver et al. 2015
	θ_S	Temperature coefficient describing shape of exponential relationship between temperature and decay rate	Unitless	1.11	Chaloner et al. 2002, Chidami and Amyot 2008, Fenoglio et al. 2005, Minshall et al. 1991, Rüegg et al. 2014, Weaver et al. 2015
	α_S	Shape parameter for carcass export rate equation	Unitless	14.0	Assumed
	$\text{DIN}_{\text{excret}}$	Rate of dissolved inorganic nitrogen excretion from adult salmon	Milligrams/gram wet mass/day	0.161	Post and Walters 2009, Wood 1995
	$\text{SRP}_{\text{excret}}$	Rate of soluble reactive phosphorus excretion from adult salmon	Milligrams/gram wet mass/day	0.032	Post and Walters 2009, Wood 1995
	$\text{DIN}_{\text{leach}}$	Rate of dissolved inorganic nitrogen leaching from salmon carcasses	Milligrams/gram wet mass/day	0.016	Assumed value (one-tenth of excretion value)
	$\text{SRP}_{\text{leach}}$	Rate of soluble reactive phosphorus leaching from salmon carcasses	Milligrams/gram wet mass/day	0.003	Assumed value (one-tenth of excretion value)
	—	Pre-spawn mortality	Unitless	0.1	Quinn 2005
	—	Salmon wet mass to AFDM conversion	Grams AFDM/gram wet mass	0.2	Elliott 1976
	$\text{Area}_{\text{redd}}$	Area of individual salmon red	Square meters	4.5	Quinn 2005
	—	Proportion of returning adult salmon spawners that are female	Unitless	0.5	Assumed
	—	Minimum suitable spawning substrate size	Meters	0.01	Quinn 2005
	—	Maximum suitable spawning substrate size	Meters	0.15	Quinn 2005

Module	Parameter	Description	Units ^a	Value	Sources
Returning salmon eggs, E	$k_{\text{stranding}}$	Stranded carcass biomass value where the terrestrial invertebrate response is half of the maximum	Grams/square meter/day	0.2	Assumed
	—	Days on spawning ground prior to spawning	Days	62.0	Assumed
	—	Lifespan post spawning	Days	20.0	Assumed
	—	Duration of habitat disturbance by salmon spawning	Days	10.0	Assumed
	—	Salmon carcass conditioning rate	Grams/gram/day	0.01	Assumed
Light	$\text{Decay}_{\text{ref},E}$	Rate of salmon egg decay at 20 °C	Grams/gram/day	0.253	Chidami and Amyot 2008
	θ_E	Temperature coefficient describing shape of exponential relationship between temperature and decay rate	Unitless	1.25	Chidami and Amyot 2008
	α_E	Shape parameter for salmon egg export rate	Unitless	18.0	Assumed
	—	Mass of individual salmon egg	Grams	0.03	Quinn 2005
	—	Egg spillage; proportion of eggs that are unsuccessfully buried during the spawning process	Unitless	0.01	Briggs 1953, Moore et al. 2008
Physical conditions	—	Proportion of (returning and added) salmon carcass biomass that is stranded in terrestrial habitats	Unitless	0.2	Assumed
	p_{reflect}	Proportion of PAR that enters water after reflection	Unitless	0.88	Julian et al. 2008
	—	Nephelometric turbidity coefficient for light attenuation	Unitless	0.17	Julian et al. 2008
	—	Acceleration due to gravity	Meters/square second	9.81	Gordon et al. 2004
	—	Water density	Kilograms/cubic meter	1000	Gordon et al. 2004
	ρ_s	Density of substrate	Kilograms/cubic meter	2.65	Gordon et al. 2004
	τ^*	Shields number	Unitless	0.045	Gordon et al. 2004
	—	Default proportion of flow in side channel	Unitless	0.1	Assumed

PAR = photosynthetically active radiation.

Note: Descriptions of reach-specific environmental parameters are found in table 2.

^a Unless otherwise noted, all units in “grams” refer to grams of ash-free dry mass (AFDM).

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