GoFish: A Next-Generation Toolkit for Modeling Migratory Fish and Environmental Risk in Estuaries

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Contents

Preface

This library provides a comprehensive, modular framework for developing and documenting agent-based models (ABMs) that simulate the movement, behavior, and environmental interactions of migratory fish in coastal aquatic systems. It is designed to support the standardization and implementation of ABMs in fisheries management, enabling researchers and practitioners to address complex environmental questions and evaluate remediation or restoration scenarios.

Motivation

The goal of this resource is to support students, researchers, and decision-makers by making agent-based modeling of migratory fish more accessible, reproducible, and applicable to real-world fisheries and habitat management challenges. By providing a standardized modular framework for key behavioral processes, this library promotes consistency, transparency, and credibility in ecological forecasting and decision support tools. It also establishes a foundation for critical conversations about the behaviors and functions represented in modelling, while supporting the empirical quantification of ecological relationships that influence movement, survival, and habitat use of migratory fish.

Chapter 1

Overview

1.1 Background

Anadromous fish species such as river herring, striped bass, and sturgeon navigate coastal and estuarine systems that are increasingly affected by human activity, climate change, and legacy contaminants. Modeling their movement and behavior at fine spatial and temporal scales requires tools that can integrate physiological stressors, environmental variability, and behavior-based decision-making.

Agent-based models are among the most powerful tools available for ecological forecasting and fisheries management, but they are also among the most complex. Their structure and computational demands can make them difficult to apply in practical management settings. Many biologists and ecologists who hold deep, species-specific expertise often have limited training in advanced programming or systems modeling. This is partly due to gaps in secondary and post-secondary education, where exposure to high-level mathematics and coding is often minimal, despite the fact that many ecological processes are governed by nonlinear systems and feedback.

As a result, traditional approaches to modeling anadromous fish frequently oversimplify or exclude key biological functions such as osmoregulation, schooling behavior, and contaminant exposure. Many existing models also lack standardized representations of these behaviors, limiting the applicability of results and reducing their usefulness for applied management. This function library was developed to address these limitations by offering modular, empirically grounded components designed for use in modeling anadromous fish. Each function is clearly documented and can be applied independently, allowing for transparent testing, modification, and reuse across a wide range of ecological scenarios and sites.

1.2 Introduction to Agent-Based Models

provide basics of ABM

1.3 Structure

Each chapter in this library corresponds to a major behavior or physiological function relevant to migratory fish, including:

- **Osmoregulation**
- **Bioaccumulation of contaminants**
- **Directional migration (landward and seaward)**
- **Schooling and Staging**
- **Selective Tidal Stream Transport**
- **Homing behavior**
- **Foraging**
- **Predator-prey interactions**
- **Spawning**

The final chapter provides guidance on how to integrate multiple functions into a complete agent-based model, demonstrating how these components work together to simulate fish behavior in dynamic coastal and estuarine systems.

Within each chapter, each function or behavior is documented using the ODD protocol (Grimm et al., 2006; 2010; 2020). The ODD (Overview, Design concepts, Details) protocol is a standardized framework for describing agent-based models. It promotes transparency in model development and ensures consistency across implementations, especially when integrating multiple behavioral or ecological functions.

- **Overview** provides the purpose of the model component, identifies the entities involved (e.g., fish agents, environmental patches), and outlines the general processes.
- **Design** concepts describe the key theoretical underpinnings such as emergence, adaptation, objectives, sensing, stochasticity, and interaction.
- **Details** specify initialization steps, input data requirements, and the rules or submodels that govern behavior.

By following the ODD protocol, this library ensures that each function is self-contained, interpretable, and ready for adaptation to a wide range of species, sites, or management scenarios.

1.4 Application Context

This library was originally developed in support of research on the influence of tidal behavior and contaminant exposure on anadromous fish in the Penobscot River Estuary. However, its modular design allows for application to other estuarine and coastal systems where fish respond to environmental changes (i.e., salinity, velocity, and pollutants).

*Can include addition project or model links here**

1.5 How to Use This Library

Each function or behavior in this library can be combined with others to build a complete agent-based model for anadromous fish. These functions are designed to be adaptable, and easily configured for different species, life stages, or site-specific conditions.

For questions, feedback, guidance on implementation, or ***interest in adding to the library****, please contact* ***Vanessa Quintana*** *at* ***mahan.vanessa98@gmail.com.***

Chapter 2

Osmoregulation Function

2.1 Overview

Osmoregulation allows migratory fish to maintain homeostasis by regulating internal ion concentrations in response to varying environmental salinities. This function simulates osmotic or ion-regulatory stress, chloride cell expression, and the metabolic energy cost of osmoregulation in a spatially explicit context.

2.2 Purpose

To simulate stress response to salinity changes for migratory fish in coastal systems by regulating chloride cell density and allocating energy toward ion-regulatory processes.

2.3 Entities, State Variables, and Scales

2.3.1 Patch Variables

Variable Name	Definition
Salinity S_{patch}	The salt concentration of a given patch, derived from hydrodynamic model inputs.

2.3.2 Agent Variables

Variable Name	Definition
acclimated-salinity S_{agent}	The salinity level the agent is currently acclimated to.
ionregulatory-stress I_{stress}	The level of stress an agent experiences when regulating ion balance due to osmotic difference.
chloride-density-min C_{min}	Minimum level of chloride cells, present even in low-stress conditions.
chloride-density-max C_{max}	Maximum level of chloride cells at high stress.
chloride-cell-density C	The current number of chloride cells expressed by the agent.
chloride-max-proliferation $R_{proliferation}$	The max number of chloride cells that can be expressed per time step.
chloride-cells-this-tick C_{tick}	The number of chloride cells created (or destroyed) in the current time step.
acclimation-rate α	The rate at which chloride cell density increases over time.
C-mid C_{mid}	The chloride cell density at which stress buffering is 50% effective.
time-since-last-osmoregulation t_{osmo}	The time elapsed since the last chloride cell regulation event.
Energy E_{agent}	The agent's total available energy for physiological functions.
E-osmo E_{osmo}	Total energy used for ion regulation (osmoregulation).
E-base E_{base}	The base energy cost per chloride cell.
E-creation $E_{creation}$	The energy cost for producing new chloride cells.
metabolic-max Met_{max}	Maximum metabolic cost for chloride cell creation.

2.4 Process Overview and Scheduling

1. Compute osmotic stress based on difference between S_{patch} and S_{agent}.
2. Adjust chloride cell density depending on time since last osmoregulation.
3. Compute energy cost of osmoregulation.
4. Deduct energy expenditure from agent's energy pool.

2.5 Design Concepts

Basic Principles: The model is based on principles of physiological ecology and osmoregulatory energetics in teleost and apterygian species. It draws from empirical findings (e.g., Allen et al., 2009; Little et al., 2023) and includes size scaling, stress buffering, and energy constraints. These principles are implemented at the submodel level (e.g., chloride proliferation, stress calculation) to simulate realistic physiological feedbacks to changes in environmental salinity.

Emergence: Ion-regulatory stress, chloride cell expression, and energy expenditure emerge from an agent's interaction with temporally and spatially variable salinity environments. These patterns are not pre-specified but arise dynamically through adaptive physiological responses.

Adaptation: Agents respond to osmotic stress by adjusting chloride cell density, a trait that buffers stress. This process allows individuals to reduce internal-external salinity gradients and maintain ion homeostasis.

Objectives: Agents seek to support survival by reducing stress and avoiding excessive energy loss through regulating chloride cell expression.

Sensing: Agents sense local salinity (S_{patch}) and compare it with their acclimated salinity (S_{agent}). They also track their own energy state and time since last osmoregulation.

Stochasticity: Acclimation may vary with α, which can be drawn from a defined range per individual to reflect physiological variation across the population.

Observation: Outputs include I_{stress}, C, E_{osmo}, and E_{agent}, all tracked per individual and exportable for analysis or visualization.

2.6 Initialization

Variable	Initialized Value	Justification
S_{patch}	user-defined for data input	This input can be user-defined realistic data values or known spatial data.
S_{agent}	35 (psu)	Assumes agents start acclimated to marine environment.
I_{stress}	1	Acclimated agents have minimal stress levels.
C	50%	Starts with partial cell density, allowing for regulation depending on environmental conditions.
C_{min}	10%	A baseline level of chloride cells is necessary for basic osmoregulatory functions.

Variable	Initialized Value	Justification
C_{max}	100%	Agents can't express more than 100% of cells.
α	0.0017 - 0.002	Osmolarity stabilization from Figure 3. in (Allen et al., 2009).
C_{mid}	50%	When cells are 50% density, stress buffering is 50% effective (Allen et al., 2009).
E_{agent}	100%	Agent starts with limited energy before migration.
E_{base}	Teleost (4%) Aptoerygian ()	Based on the **branchial cost** (Little et al., 2023; Kirschner, 1993).
Met_{max}	Teleost (3.5%)	Based on the intestinal and renal cost & size of agent (Little et al., 2023; Kirschner, 1993).
k	-0.75	Scaling component for body mass is negative (Kirschner, 1993) and follows Kleiber's Law.

2.7 Submodels

2.7.1 Osmotic Stress

Ion-regulatory stress (I_{stress}) is calculated based on the difference between an agent's acclimated salinity and the ambient patch salinity, adjusted by the chloride cell buffering effect:

$$I_{stress} = \frac{\log_{10}(1 + |S_{agent} - S_{patch}|) \cdot 10}{1 + e^{-2\cdot(C/C_{mid})}}$$

Stress is capped within the range [1, 10], and may be reduced slightly over time if salinity remains stable and chloride density is sufficient:

$$I_{stress} = I_{stress} \cdot 0.98 \quad \text{if conditions are stable and } C > C_{min}$$

Agents also slowly shift their acclimated salinity toward ambient salinity when conditions have been stable for several time steps:

$$S_{agent} = S_{agent} + (S_{patch} - S_{agent}) \cdot 0.02$$

Where:

- I_{stress} is ion-regulatory (osmotic) stress, scaled between 1 and 10.
- S_{agent} is the agent's acclimated salinity.
- S_{patch} is the environmental salinity at the current patch.
- C is the chloride cell density (percent of maximum).
- C_{mid} is the density at which buffering is 50% effective.

2.7.2 Chloride Cell Density

Chloride cell proliferation is driven by the level of ion-regulatory stress the agent experiences when encountering a difference in salinity. The greater the stress, the higher the target chloride density the agent attempts to reach, up to a maximum threshold. Agents adjust their chloride cell density based on their current ion-regulatory stress and acclimation status. Chloride cells are not adjusted unless the agent's energy exceeds 25%.

The chloride cell density is based on stress:

$$C_{target} = C_{min} + (C_{max} - C_{min}) \cdot \left(\frac{I_{stress}}{10}\right)$$

If salinity conditions have remained stable for an extended period (e.g., 288 ticks), \(C_{target}\) is slightly reduced to reflect partial downregulation of chloride cells due to long-term acclimation:

$$C_{target} = C_{target} \cdot 0.99 \quad \text{if stable}$$

Chloride cell density then approaches the target using a double-rate adjustment and capped maximum rate of change:

$$\Delta C = \left(C_{target} - C_{current}\right) \cdot \left(2 \cdot R_{proliferation}\right)$$

$$\Delta C = \max\left(-R_{max}, \min(R_{max}, \Delta C)\right)$$

If the agent has low energy ($\leq 50\%$), the adjustment rate is halved:

$$\Delta C = \Delta C \cdot 0.5 \quad \text{if energy is low}$$

Finally, the chloride cell density is updated and constrained between C_{min} and C_{max}:

$$C_{new} = \max(C_{min}, \min(C_{max}, C_{current} + \Delta C))$$

This ensures that the agent does not overshoot the physiologically realistic limit of chloride cell density, while still responding to osmotic stress.

Chloride density is only recalculated after a given acclimation interval:

$$t_{osmo} \geq \alpha^{-1}$$

After updating, the acclimation timer is reset:

$$t_{osmo} = 0$$

This prevents agents from recalculating chloride density every time step and allows for controlled, realistic responses to prolonged stress and salinity changes.

Where:

- I_{stress} is the ion-regulatory stress, scaled from 1 to 10.
- C_{target} is the desired chloride cell density based on stress level.
- C_{min} and C_{max} are the bounds for chloride cell density.
- $R_{proliferation}$ determines the **maximum allowable increase** per time step.
- ΔC is the rate of change in chloride cell expression.
- $R_{max} = (C_{max} - C_{min}) \cdot R_{proliferation}$
- C_{new} is the percent of new chloride cell expression.
- α is the acclimation rate constant.
- t_{osmo} represents time since the last osmoregulation event.

Osmoregulation Energy

Metabolic cost related to size:

$$E_{creation} = Met_{max} * (\frac{M}{M_{max}})^k$$

Where:

- $E_{creation}$ is the energy cost of chloride cell creation
- Met_{max} is the maximum metabolic cost of the agent
- M is equal to the agent's size, where smaller fish spend proportionally more energy on osmoregulation (Little et al., 2023)
- M_{max} is the maximum mass of an agent within the population
- k follows size-dependent variation in energy allocation, consistent with a negative scaling exponent.

Energy required for ion regulation:

$$E_{osmo} = (E_{base} \cdot C) + (E_{creation} \cdot C_{tick})$$

Where:

- E_{base} represents the energy cost per chloride cell for maintenance.
- C is the current chloride density.
- $E_{creation}$ represents the cost of producing new chloride cells.
- C_{tick} is the number of newly created chloride cells in the current time step.

2.7.3 Energy Balance

Agents balance energy to osmoregulate with total energy allowance:

$$E_{agent} = E_{agent} - E_{osmo}$$

Where:

- E_{agent} is the total energy of the agent.
- E_{osmo} is the energy consumed during osmoregulation.

Chapter 3

Thermoregulation Function

3.1 Overview

This model simulates thermoregulation behavior and physiological consequences in migratory fish agents. Each agent experiences temperature-dependent effects on movement, survival, and performance based on its local environment. Agents have defined thermal traits including an optimal temperature, a minimum viable temperature, and a maximum tolerable temperature. These constraints influence swimming speed and determine whether survival is possible in the current patch.

3.2 Purpose and Patterns

This submodel captures ecologically grounded thermoregulatory behavior in migratory fish by simulating how temperature influences movement, survival, and physiological performance during migration and staging.

- Agents experience thermal stress based on deviations from their optimal temperature, with stress scaling nonlinearly as conditions approach species-specific tolerance thresholds.
- Swimming speed is reduced as environmental temperature deviates from thermal optima, reflecting empirical performance curves and diminished locomotor efficiency at suboptimal temperatures.
- Agents calculate energy expenditure associated with thermoregulation, with increased metabolic cost arising from reduced swimming efficiency under thermal stress.

- When thermal stress exceeds a threshold, agents evaluate neighboring patches and relocate to cooler or warmer areas to minimize physiological strain.
- Agents track cumulative time spent beyond minimum and maximum viable temperature thresholds, and mortality occurs after sustained exposure to lethal conditions.
- This model supports the analysis of thermal niche constraints, temperature-driven habitat selection, and the vulnerability of fish to extreme temperature events in estuarine systems.

3.3 Entities, State Variables, and Scales

3.3.1 Spatial and Temporal Scales

- **Spatial Unit**: Patch (3 m x 3 m resolution)
- **Temporal Unit**: 5-minute time steps (`tick`)

3.3.2 Patch Variables

Variable Name	Definition
Temperature T_{patch}	The temperature of a given patch, derived from hydrodynamic model inputs.

3.3.3 Agent Variables

Variable Name	Definition
Optimal Temperature T_{opt}	Optimal performance temperature
Minimum Viable Temperature T_{min}	Minimum viable temperature for survival
Maximum Viable Temperature T_{max}	Maximum viable temperature for survival
swimming speed V_{agent}	The speed at which a prey agent is moving
corrected speed V_{corr}	The corrected speed from thermal implications
time below minimum t_{min}	Tracks cumulative cold exposure duration
time above maximum t_{max}	Tracks cumulative heat exposure duration

Variable Name	Definition
energy E_{agent}	Metabolic cost associated with thermoregulation
swimming speed V_{agent}	The current swimming speed of the agent.
acclimation rate λ	Rate at which agent acclimates to temperature based on size, age, and species.

3.4 Process Overview and Scheduling

1. **Thermal Stress Calculation**
   Each agent calculates thermal stress based on the deviation between the current patch temperature and its individual thermal optimum. Stress is scaled nonlinearly to reflect increasing physiological strain near temperature limits.

2. **Acclimation**
   Agents gradually adjust their optimal temperature toward the current patch temperature using a fixed acclimation rate, simulating physiological plasticity over time.

3. **Thermal Mortality Check**
   Agents track cumulative exposure to lethal temperatures. If the patch temperature falls below the agent's minimum threshold or exceeds its maximum threshold for more than three consecutive time steps, the agent dies.

4. **Swimming Speed Correction**
   Swimming speed is modified using a thermal correction factor derived from the agent's deviation from its optimal temperature. This adjustment affects movement performance and downstream behaviors.

5. **Thermal Avoidance**
   If thermal stress exceeds a threshold value (e.g., $S_{thermal} > 7$), agents evaluate neighboring patches and move to the patch with the lowest thermal stress.

6. **Energy Cost Adjustment**
   Swimming energy cost is scaled based on the ratio of thermally corrected speed to the agent's base swimming speed. This reflects increased metabolic effort under suboptimal thermal conditions.

3.5 Design Concepts

Basic Principles: Agents are ectothermic and thermally constrained. Movement and survival depend on physiological performance at environmental temperatures.

Emergence: Spatial thermal gradients produce differential survival, movement, and performance outcomes across the landscape.

Adaptation: Agents modify their optimal temperature slowly to match local conditions, simulating physiological acclimation.

Objectives: Agents attempt to avoid lethal temperatures and maintain performance within their thermal niche while minimizing energy loss.

Sensing: Agents sense local patch temperature and compare it to their thermal limits and optimal range.

Interaction: Agents interact with their environment by relocating to lower-stress patches and adjusting internal states accordingly.

Observation: Thermal stress, adjusted swimming speed, energy cost, cumulative heat/cold exposure, and thermal mortality can be tracked per agent.

3.6 Initialization

Variable	Initialized Value	Justification
T_{min}	Species-specific threshold	Based on empirical lower thermal limit for survival
T_{opt}	Species- or life stage–specific value	Reflects thermal preference; varies by developmental stage or habitat
T_{max}	Species-specific threshold	Based on empirical upper thermal limit for survival
T_{patch}	Hydrodynamic model input	External environmental condition updated each tick
$S_{thermal}$	1	No stress at initialization if $T_{patch} = T_{opt}$
t_{min}	0	No prior exposure to lethal cold stress
t_{max}	0	No prior exposure to lethal heat stress
V_{agent}	Size-scaled base speed	Initial swimming speed assuming full capacity
E_{agent}	100	No thermal deviation at model start
E_{swim}	Size-scaled base swim cost	Scales with body size; used in movement energy balance
E_{swim}^{corr}	Equal to E_{swim}	No thermal penalty at initialization
λ	0.01–0.05 (user-defined)	Acclimation rate controls speed of physiological adjustment

3.7 Submodels

3.7.1 Thermal Stress

Thermal stress is scaled exponentially between 1 (optimal) and 10 (at or beyond minimum or maximum viable temperatures).

$$S_{thermal} = 1 + 9 \cdot \left(\frac{|T_{patch} - T_{opt}|}{\max(|T_{opt} - T_{min}|, |T_{max} - T_{opt}|)} \right)^k$$

Where:

- $S_{thermal}$ is the thermal stress score.
- T_{patch} is the current patch temperature.
- T_{opt}, T_{min}, T_{max} are the agent's thermal preferences.
- k is an exponent controlling the steepness of the stress curve.

3.7.2 Acclimation and Plasticity

$$T_{opt}(t+1) = T_{opt}(t) + \lambda \cdot (T_{patch} - T_{opt}(t))$$

Where:

- T_{opt} gradually shifts toward T_{patch}
- λ is the acclimation rate (e.g. 0.01-0.05)

3.7.3 Temperature-Adjusted Swimming Speed (place inside migration function(s))

$$V_{corr} = V_{agent} \cdot \left(1 - \left| \frac{T_{patch} - T_{opt}}{T_{opt}} \right| \right)$$

Where:

- V_{agent} is the agent's swimming speed.
- V_{corr} is the thermal corrected speed.
- T_{patch} is the temperature of the current patch.
- T_{opt} is the agent's optimal temperature.

3.7.4 Thermal-Avoidance Movement (place inside migration function(s))

Agents check thermal stress in their current patch. If $S_{thermal} > 7$, they evaluate neighboring patches. The agent moves to the neighbor with the lowest $S_{thermal}$ value.

Where:

- $S_{thermal}$ is the thermal stress score.

3.7.5 Thermal Mortality Thresholds (place inside migration function(s))

t_{min} and t_{max} are incremented when temperature thresholds are exceeded:

$$\text{if } T_{patch} < T_{min} \text{ for more than 3 consecutive time steps,} \quad \text{agent dies}$$

$$\text{if } T_{patch} > T_{max} \text{ for more than 3 consecutive time steps,} \quad \text{agent dies}$$

Where:

- T_{min} is the minimum viable temperature.
- T_{max} is the maximum tolerable temperature.

3.7.6 Energy Consumption (place inside migration function(s))

Acclimation energy cost:

$$E_{acclimation} = \phi \cdot |T_{patch} - T_{opt}|$$

Where:

- $E_{acclimation}$ is the energy cost for physiological acclimation.
- T_{patch} is the current patch temperature.
- ϕ is a scaling constant for acclimation cost (e.g., 0.01–0.05).
- T_{opt} is the agent's current thermal optimum.

This energy consumption corrects the energy used based on the V_{corr}:

$$E_{swim}^{corr} = E_{swim} \cdot \left(\frac{V_{agent}}{V_{corr}} \right)$$

Where:

- E_{swim}^{corr} is the corrected energy cost for movement.
- E_{swim} is swimming-related energetic inefficiency from thermal deviation.
- V_{agent} is the agent's swimming speed.
- V_{corr} is the thermal corrected speed.

Total energy balance:

$$E_{agent} = E_{agent} - (E_{swim}^{corr} + E_{acclimation})$$

Where:

- E_{swim}^{corr} accounts for temperature-related movement inefficiency.
- $E_{acclimation}$ accounts for metabolic costs of internal physiological adjustment.
- E_{agent} is the updated available energy of the agent.

Chapter 4

Mercury Contamination Bioaccumulation Function

4.1 Overview

This function simulates exposure and uptake risk of mercury (Hg) and methylmercury (MeHg) for migratory fish navigating contaminated aquatic environments. The model accounts for spatial and temporal variation in contaminant concentrations and includes physiological modulation based on ion-regulatory stress and suspended particulate matter (SPM).

4.2 Purpose

To evaluate contaminant exposure and bioaccumulation risk in migratory fish due to mercury and methylmercury during migration through estuarine or coastal systems using stress.

4.3 Entities, State Variables, and Scales

4.3.1 Global Variables

Variable	Initialized Value	Justification
MeHg-Threshold $MeHg_{threshold}$	15 ug/kg	10% of mercury concentration (Gaudet et al., 1995)
Hg-Threshold $Hg_{threshold}$	150 ug/kg	(Gaudet et al., 1995) ((NOAA) National Oceanic and Atmospheric Administration, 1990)

4.3.2 Patch Variables

Variable Name	Definition
Mercury Hg_{patch}	The mercury concentration of a patch.
Methylmercury $MeHg_{patch}$	The methylmercury concentration of a patch.
Suspended-particulate-matter SPM_t	The concentration of suspended particulate matter (SPM) for a given patch, derived from hydrodynamic model inputs, which change temporally.

4.3.3 Agent Variables

Variable Name	Definition
stress S	The level of stress an agent experiences when moving.
Hg-exposure-duration Hg_{exp_t}	The amount of time an agent is exposed to mercury above healthy levels.
MeHg-exposure-duration $MeHg_{exp_t}$	The amount of time an agent is exposed to methylmercury above healthy levels.
Hg-uptake-risk Hg_{risk}	The risk associated for uptake of mercury.
MeHg-uptake-risk $MeHg_{risk}$	The risk associated for uptake of methylmercury.
Hg-exposure Hg_t	The amount of mercury exposed during current time step.

Variable Name	Definition
MeHg-exposure $MeHg_t$	The amount of methlymercury exposed during current time step.
Hg-exposure-total Hg_{net}	The net sum of mercury exposed to during migration.
MeHg-exposure-total $MeHg_{net}$	The net sum of methylmercury exposed to during migration.

4.4 Process Overview and Scheduling

1. Evaluate current patch concentrations of mercury and methylmercury.
2. Determine whether these exceed defined toxicity thresholds.
3. Calculate exposure duration (if thresholds exceeded).
4. Compute bioaccumulation risk based on contaminant levels, stress, and SPM.
5. Update cumulative exposure totals.

4.5 Design Concepts

Basic Principles: this model is grounded in toxicokinetics and ecological exposure theory. It draws on empirical literature (e.g., Gaudet et al. 1995, NOAA 1990) and integrates physiological stress responses with contaminant risk, reflecting a mechanistic understanding of exposure and bioaccumulation dynamics.

Emergence: While exposure durations and patch-level concentrations are direct inputs, the exposure patterns (Hg_t, $MeHg_t$), cumulative exposure totals (Hg_{net}, $MeHg_{net}$), and risk profiles (Hg_{risk}, $MeHg_{risk}$) emerge from agent movement across spatially and temporally variable environments and their physiological state, which arise from behavioral-environmental interactions over time.

Adaptation: Agents adaptively accumulate risk based on their movement decisions, stress state, and encountered contaminant levels, simulating a physiological feedback process.

Objectives: Agents do not explicitly seek to minimize risk, but their cumulative exposure and risk profiles can be used to evaluate environmental quality and cumulative toxicity risk for migratory fish.

Sensing: Agents sense the local contaminant levels (Hg_{patch}, $MeHg_{patch}$), suspended particulate matter (SPM_t), and their own stress state (S).

Stochasticity: Randomized initial conditions (e.g., Hg and MeHg levels) may introduce variability in exposure patterns.

Observation: Exposure variables (Hg_t, $MeHg_t$), cumulative exposure (Hg_{net}, $MeHg_{net}$), and risk scores (Hg_{risk}, $MeHg_{risk}$) are collected per agent and can be exported for analysis.

4.6 Initialization

Variable	Initialized Value	Justification
S	user-defined stress function	Changes in an agent's environment can induce a stress response, and can be induced by the user or environmental response.
Hg_{patch}	user-defined or data input	This input can be user-defined realistic data values or known spatial data.
$MeHg_{patch}$	user-defined for data input	This input can be user-defined realistic data values or known spatial data.

4.7 Submodels

4.7.1 Exposure Duration

The cumulative number of time steps an agent is exposed to mercury and methylmercury above specified environmental thresholds:

$$Hg_{exp_t} = Hg_{exp_t} + 1 \quad \text{if } Hg_{patch} > Hg_{threshold}$$

$$MeHg_{exp_t} = MeHg_{exp_t} + 1 \quad \text{if } MeHg_{patch} > MeHg_{threshold}$$

Where:

- Hg_{exp_t} is the total number of time steps exposed to mercury above threshold.
- Hg_{patch} is the mercury concentration at the current patch location.
- $Hg_{threshold}$ is the defined mercury toxicity threshold.
- $MeHg_{exp_t}$ is the total number of time steps exposed to methylmercury above threshold.
- $MeHg_{patch}$ is the methylmercury concentration at the current patch location.
- $MeHg_{threshold}$ is the defined methylmercury toxicity threshold.

4.7.2 Bioaccumulation Risk

Estimate the bioaccumulation risk associated with mercury and methylmercury, where risk increases with contaminant concentration, ion-regulatory stress, and suspended particulate matter (SPM):

$$Hg_{risk} = \sum_{t=1}^{T} Hg_{normalized} * (1 + S) * (1 + SPM_t)$$

$$MeHg_{risk} = \sum_{t=1}^{T} MeHg_{normalized} * (1 + S) * (1 + SPM_t)$$

Where:

- Hg_{risk} is the instantaneous mercury uptake risk.
- $MeHg_{risk}$ is the instantaneous methylmercury uptake risk.
- $Hg_{normalized}$ is the normalized Hg concentration (scaled 0–1) at each time step.
- $MeHg_{normalized}$ is the normalized MeHg concentration (scaled 0–1).
- S is the stress level of the agent.
- SPM_t is the suspended particulate matter concentration at the patch for that time step.

4.7.3 Exposure to Contamination

Agents record exposure to mercury and methylmercury only when concentrations exceed threshold values. These values are stored per time step and accumulated over time to assess total contaminant burden.

Mercury:

$$Hg_t = \begin{cases} Hg_{patch}, & \text{if } Hg_{patch} > Hg_{threshold} \\ 0, & \text{otherwise} \end{cases}$$

$$Hg_{net} = \sum_{t=1}^{T} Hg_t$$

Where:

- Hg_t is the mercury exposure in ng/g for current time step
- Hg_{net} is the cumulative mercury exposure in ng/g
- Hg_{patch} is the mercury concentration for the agent's current patch

Methylmercury:

$$MeHg_t = \begin{cases} MeHg_{patch}, & \text{if } MeHg_{patch} > MeHg_{threshold} \\ 0, & \text{otherwise} \end{cases}$$

$$MeHg_{net} = \sum_{t=1}^{T} MeHg_t$$

Where:

- $MeHg_t$ is the level of methylmercury exposure in ng/g for current time step
- $MeHg_{net}$ is the cumulative methylmercury exposure in ng/g
- $MeHg_{patch}$ is the methylmercury concentration for the agent's current patch

Chapter 5

Landward Migration Behavior

5.1 Overview

This function simulates landward (upstream) migratory behavior of fish navigating riverine and estuarine systems. Agents face resistance from environmental water velocity and incur energetic costs that scale with flow conditions and their size.

5.2 Purpose

To model how migratory fish respond to varying riverine and tidal velocities by calculating effective swimming speed, difficulty of movement, and the energetic cost associated with upstream migration.

5.3 Entities, State Variables, and Scales

5.3.1 Global Variables

Variable	Initialized Value	Justification
minimum-velocity V_{min}	Calculated from V_{patch} over the simulation period.	Minimum river velocity based on hydrodynamic observations.

Variable	Initialized Value	Justification
maximum-velocity V_{max}	Calculated from V_{patch} over the simulation period.	Maximum river velocity based on hydrodynamic observations.

5.3.2 Patch Variables

Variable Name	Definition
Velocity V_{patch}	The along-channel velocity of a given patch, derived from hydrodynamic model inputs, where positive values are in the landward direction and negative values are in the seaward direction.

5.3.3 Agent Variables

Variable Name	Definition
size M_{agent}	The size of an agent.
M-max M_{max}	Maximum size found within the agent's population.
swimming-speed V_{agent}	The current swimming speed of the agent.
maximum-speed $swim_{max}$	The maximum sustained speed of the agent.
difficulty-factor D_f	The level of difficulty an agent experiences when swimming.
energy E_{agent}	The total energy an agent has.
swimming-energy-cost $Swim_{base}$	The base energy cost of swimming.
net-swimming-cost E_{swim}	The total energy expenditure for swimming.
heading $\hat{u}$	The direction agent is facing or "headed towards"
Y-position $\vec{Y}_t$	This is the agent's position in the Y plane

5.4 Process Overview and Scheduling

1. Determine effective swimming speed based on flow velocity and agent energy.
2. Compute swimming difficulty factor using normalized velocity.
3. Calculate movement direction and update position.
4. Deduct swimming energy cost from agent's energy pool.

5.5 Design Concepts

Basic Principles: This model builds on hydrodynamic constraints and energetic theory. It assumes that swimming against current imposes increased metabolic demands and that movement is energetically limited by individual traits.

Emergence: Movement trajectories ($\hat{u}$) and energy (E_{agent}) depletion emerge from the interaction between local flow conditions, fish traits, and directional behavior.

Objectives: Agents aim to migrate upstream. While they do not explicitly optimize, their movement is shaped by their capacity to overcome current velocity V_{patch}).

Sensing: Agents detect the local water velocity (V_{patch}) and use it to update their speed (V_{agent}) and effort (D_f).

Observation: Agent positions ($\vec{Y}_t$)and energy states can be tracked per time step to analyze migration success and efficiency.

5.6 Initialization

Variable	Initialized Value	Justification
V_{patch}	user-defined for data input	This input can be user-defined realistic data values or known spatial data.
M_{agent}	user-defined and species-specific	Representative body length of a migrating agent.

Variable	Initialized Value	Justification
M_{max}	user-defined and species-specific	Based on the maximum body length in the agent's population.
V_{agent}	$\frac{V_{max}}{2}$	Fish begin migration with a moderate swimming speed relative to their maximum capacity.
$swim_{max}$	$1.5 - 3\frac{bodylengths}{sec}$	Typical value for sustained swimming speed in small pelagic fish (refer to Videler, 1993).
E_{agent}	100%	Agent starts migration at 100% relative energy capacity.
$swim_{base}$	$0.02 \cdot \frac{M_{agent}}{M_{max}}^{k}$	Scales locomotion cost nonlinearly with size; can be calibrated.
k	0.75	Energetic scaling component that follows Kleiber's Law.
$\hat{u}$	0°	Unit vector in the upstream direction

5.7 Submodels

5.7.1 Swimming Speed

Agents calculate swimming speed based on their available energy and hydrodynamic resistance:

$$V_{agent} = \frac{swim_{max} * E_{agent}}{100} - (-k \cdot |V_{patch}|)$$

Where:

- $swim_{max}$ is the maximum sustained swimming speed of the agent.
- V_{patch} is the environmental velocity at the agent's current patch.
- V_{agent} is the effective swimming speed of the agent.

- E_{agent} is the agent's available energy percentage (0-100%).
- k is a scaling factor that determines how velocity influences swimming effort.

5.7.2 Swimming Difficulty

The difficulty factor quantifies the additional energetic burden of swimming against different velocity conditions. In this case, difficulty is calculated using a normalized velocity-based proxy that scales difficulty from 1-10 between observed flow extremes.

$$D_f = 1 + 9 \cdot \left(\frac{\left(\frac{|V_{patch}|}{swim_{max} \cdot \left(\frac{M_{agent}}{M_{max}} \right)} \right)^k - V_{min}}{V_{max} - V_{min}} \right)$$

Where:

- M_{agent} is the size of the agent.
- M_{max} is the maximum size within the agent's population.
- $swim_{max}$ is the maximum swimming speed capability of the agent.
- V_{max} is the maximum depth-averaged water velocity observed within the simulation.
- V_{min} is the minimum depth-averaged water velocity observed within the simulation.
- V_{patch} is the depth-averaged water velocity for the agent's current patch.
- D_f is the swimming difficulty factor.

Biological Justification:

When $V_{patch} \approx 0$, difficulty is moderate.

When $V_{patch} < 0$, difficulty increases because the fish is actively swimming against the current.

When $V_{patch} > 0$, difficulty is minimal as fish drift with the current.

5.7.3 Swimming Movement

During landward migration, agents orient upstream and move forward based on their calculated swimming speed:

$$\vec{Y}_{t+1} = \vec{Y}_t + V_{agent} \cdot \hat{u}$$

Where:

- $\vec{Y}_t$ is the agent's current spatial position.
- $\vec{Y}_{t+1}$ is the agent's updated spatial position after one time step.
- V_{agent} is the swimming speed calculated from energy and difficulty.
- $\hat{u}$ is the unit vector in the landward direction.

5.7.4 Swimming Energy

Swimming energy cost is determined by the base cost of locomotion scaled by a difficulty factor raised to a scaling factor. This allows energy expenditure to increase non-linearly as flow resistance increases.

$$E_{swim} = Swim_{base} \cdot D_f^k$$

Where:

- E_{swim} is the energy cost of swimming.
- $Swim_{base}$ is the base swimming cost based on agent size.
- D_f is the swimming difficulty factor.
- k is the scaling factor, reflecting nonlinear energy demand.

5.7.5 Energy Balance

Agents balance energy to swim with total energy allowance:

$$E_{agent} = E_{agent} - E_{swim}$$

Where:

- E_{agent} is the current energy available to the agent.
- E_{swim} is the energy cost of swimming in this time step.

Chapter 6

Seaward Migration Behavior

6.1 Overview

This function simulates seaward (downstream) migratory behavior of fish navigating riverine and estuarine systems. Agents face resistance from tidal flows and benefit from downstream riverine flows. The function models effective swimming speed, the difficulty of movement, and energetic costs during seaward migration.

6.2 Purpose

To model how migratory fish respond to along-channel velocity when traveling seaward by determining swimming speed, hydrodynamic difficulty, and the energetic cost of downstream migration.

6.3 Entities, State Variables, and Scales

6.3.1 Global Variables

Variable	Initialized Value	Justification
minimum-velocity V_{min}	Calculated from V_{patch} over the simulation period.	Minimum river velocity based on hydrodynamic observations.
maximum-velocity V_{max}	Calculated from V_{patch} over the simulation period.	Maximum river velocity based on hydrodynamic observations.

6.3.2 Patch Variables

Variable Name	Definition
Velocity V_{patch}	The along-channel velocity of a given patch, derived from hydrodynamic model inputs, where positive values are in the landward direction and negative values are in the seaward direction.

6.3.3 Agent Variables

Variable Name	Definition
size M_{agent}	The size of an agent.
M-max M_{max}	Maximum size found within the agent's population.
swimming-speed V_{agent}	The current swimming speed of the agent.
maximum-speed $swim_{max}$	The maximum sustained speed of the agent.
difficulty-factor D_f	The level of difficulty an agent experiences when swimming.
energy E_{agent}	The total energy an agent has.
swimming-energy-cost $Swim_{base}$	The base energy cost of swimming.
net-swimming-cost E_{swim}	The total energy expenditure for swimming.
heading $\hat{u}$	The direction agent is facing or "headed towards"
Y-position $\vec{Y}_t$	This is the agent's position in the Y plane

6.4 Process Overview and Scheduling

1. Determine effective swimming speed based on flow velocity and agent energy.
2. Compute swimming difficulty factor using normalized velocity.
3. Calculate movement direction and update position.
4. Deduct swimming energy cost from agent's energy pool.

6.5 Design Concepts

Basic Principles: This model builds on hydrodynamic constraints and energetic theory. It assumes that swimming against current imposes increased metabolic demands and that movement is energetically limited by individual traits.

Emergence: Movement trajectories ($\hat{u}$) and energy (E_{agent}) depletion emerge from the interaction between local flow conditions, fish traits, and directional behavior.

Objectives: Agents aim to migrate downstream. While they do not explicitly optimize, their movement is shaped by their capacity to overcome current velocity V_{patch}).

Sensing: Agents detect the local water velocity (V_{patch}) and use it to update their speed (V_{agent}) and effort (D_f).

Observation: Agent positions ($\vec{Y}_t$)and energy states can be tracked per time step to analyze migration success and efficiency.

6.6 Initialization

Variable	Initialized Value	Justification
V_{patch}	user-defined for data input	This input can be user-defined realistic data values or known spatial data.
M_{agent}	user-defined and species-specific	Representative body length of a migrating agent.

Variable	Initialized Value	Justification
M_{max}	user-defined and species-specific	Based on the maximum body length in the agent's population.
V_{agent}	$\frac{V_{max}}{2}$	Fish begin migration with a moderate swimming speed relative to their maximum capacity.
$swim_{max}$	$1.5 - 3\frac{bodylengths}{sec}$	Typical value for sustained swimming speed in small pelagic fish (refer to Videler, 1993).
E_{agent}	100%	Agent starts migration at 100% relative energy capacity.
$swim_{base}$	$0.02 \cdot \frac{M_{agent}}{M_{max}}^{k}$	Scales locomotion cost nonlinearly with size; can be calibrated.
k	0.75	Energetic scaling component that follows Kleiber's Law.
$\hat{u}$	180°	Unit vector in the downstream direction

6.7 Submodels

6.7.1 Swimming Speed

$$V_{agent} = \frac{V_{max} * E_{agent}}{100} - (k \cdot |V_{patch}|)$$

Where:

- V_{max} is the maximum sustained swimming speed of the agent.
- V_{patch} is the environmental velocity at the agent's current patch.
- V_{agent} is the effective swimming speed of the agent.
- E_{agent} is the agent's available energy percentage (0-100%).
- k is a scaling factor that determines how velocity influences swimming effort.

6.7.2 Swimming Difficulty

The difficulty factor quantifies the additional energetic burden of swimming against different velocity conditions. In this case, difficulty is calculated using a normalized velocity-based proxy that linearly scales difficulty from 1-10 between observed flow extremes.

$$D_f = 1 + 9 \cdot \left(\frac{\left(\frac{|V_{patch}|}{V_{max} \cdot \left(\frac{M_{agent}}{M_{max}} \right)} \right)^k - V_{min}}{V_{max} - V_{min}} \right)$$

Where:

- M_{agent} is the size of the agent.
- M_{max} is the maximum size within the agent's population.
- V_{max} is the maximum swimming speed capability of the agent.
- V_{max} is the maximum depth-averaged water velocity observed within the simulation.
- V_{min} is the minimum depth-averaged water velocity observed within the simulation.
- V_{patch} is the depth-averaged water velocity for the agent's current patch.
- D_f is the swimming difficulty factor.

Biological Justification

- When $V_{patch} \approx 0$, difficulty is moderate.
- When $V_{patch} < 0$, difficulty increases because the fish is actively swimming against the current.
- When $V_{patch} > 0$, difficulty is minimal as fish drift with the current.

6.7.3 Swimming Movement

During landward migration, agents orient upstream and move forward based on their calculated swimming speed:

$$\vec{Y}_{t+1} = \vec{Y}_t + V_{agent} \cdot \hat{u}$$

Where:

- $\vec{Y}_t$ is the agent's current spatial position.
- $\vec{Y}_{t+1}$ is the agent's updated spatial position after one time step.
- V_{agent} is the swimming speed calculated from energy and difficulty.
- $\hat{u}$ is the unit vector in the seaward direction (180° heading, downstream).

6.8 Swimming Energy

Swimming energy cost is determined by the base cost of locomotion scaled by a difficulty factor raised to a power. This allows energy expenditure to increase non-linearly as flow resistance increases.

$$E_{swim} = Swim_{base} \cdot D_f^k$$

Where:

- E_{swim} is the energy cost of swimming.
- $Swim_{base}$ is the base swimming cost based on agent size.
- D_f is the swimming difficulty factor.
- k is the scaling exponent, reflecting nonlinear energy demand.

6.8.1 Energy Balance

Fish allocate energy efficiently, balancing osmoregulation with other survival functions.

$$E_{agent} = E_{agent} - E_{swim}$$

Where:

- E_{agent} is the current energy available to the agent.
- E_{swim} is the energy cost of swimming in this time step.

Chapter 7

Schooling Behavior

7.1 Overview

7.2 Purpose

7.3 Entities, State Variables, and Scales

7.3.1 Patch Variables

Variable Name	Definition

7.3.2 Agent Variables

Variable Name	Definition

7.4 Process Overview and Scheduling

1.
2.
3.
4.

7.5 Design Concepts

Basic Principles:

Emergence:

Adaptation:

Objectives:

Learning:

Prediction:

Sensing:

Interaction:

Stochasticity:

Collectives:

Observation:

7.6 Initialization

Variable	Initialized Value	Justification

7.7 Submodels

Chapter 8

Selective Tidal Stream Transport

8.1 Overview

Selective Tidal Stream Transport (STST) is a behavioral strategy that enables agents to conserve energy by passively drifting with the current. It is triggered when the along-channel velocity of the patch exceeds the agent's effective swimming speed, and that speed is below a species-specific minimum threshold. Once engaged, agents align with the tidal current and are carried downstream or upstream, depending on flow velocity. STST reduces the metabolic cost of movement by substituting active swimming with passive transport. This behavior persists for a limited duration or until swimming ability improves, after which agents resume directional migration.

8.2 Purpose

To simulate a passive energy-conserving behavior in migratory fish that allows them to use tidal currents to move when swimming capacity is insufficient to overcome flow velocities.

8.3 Entities, State Variables, and Scales

8.3.1 Patch Variables

Variable Name	Definition
Velocity V_{patch}	The along-channel velocity of a given patch, derived from hydrodynamic model inputs, where positive values are in the landward direction and negative values are in the seaward direction.
tidal-transport-in-patch	Count of agents exhibiting tidal stream transport within a patch (for habitat quality analysis).

8.3.2 Agent Variables

Variable Name	**Definition**
energy E_{agent}	Total energy available to the agent.
swimming energy E_{swim}	Energy expenditure from movement per time step.
base swim energy $swim_{base}$	Baseline energy cost of movement.
swimming difficulty D_f	Velocity-based proxy representing hydrodynamic resistance.
in-STST? $STST_?$	Boolean value indicating if the agent is actively in STST.
swimming speed V_{agent}	The effective swimming speed of the agent.
minimum threshold speed $Speed_{min}$	The minimum speed at which an agent will move.

8.4 Process Overview and Scheduling

1. Compare swimming speed (V_{agent}) with flow speed (V_{patch}).
2. If $|V_{patch}| > V_{agent}$ and $V_{agent} \leq Speed_{min}$, enter STST.
3. In STST: align with current, update position via drift, apply reduced energy cost.
4. If $V_{agent} > Speed_{min}$, exit STST and resume active swimming.

8.5 Design Concepts

Basic Principles: Selective tidal stream transport is based on behavioral ecology and energetics, simulating the tradeoff between active swimming and energy conservation through passive transport.

Emergence: Passive drift behavior and resulting migration paths emerge from agent-flow interactions and individual swimming limitations.

Adaptation: Agents adapt their mode of movement based on their swimming ability relative to environmental flow, dynamically choosing energy-efficient strategies.

Objectives: Agents seek to minimizing energy loss in strong flows.

Sensing: Agents sense their own V_{agent} and the V_{patch} to determine whether passive drift is needed.

Observation: Records STST patch events , energy expenditure (E_{agent}), and displacement are logged to analyze behavior across flow regimes.

8.6 Initialization

Variable	Initialized Value	Justification
V_{agent}	Based on size, energy, and difficulty factor	Reflects agent's swimming capability based on metabolic limits.
$swim_{min}$	Species-specific parameter	Represents the minimum sustained swimming velocity of the agent.
$swim_{max}$	Species-specific parameter	Represents the maximum sustained swimming velocity of the agent.
E_{agent}	100	Assumes full energy at the start of simulation or at spawning.
$swim_{base}$	$0.02 \cdot \frac{M_{agent}}{M_{max}}^{k}$	Scales locomotion cost nonlinearly with size; can be calibrated.

8.7 Submodels

8.7.1 Trigger Conditions for STST

Agents compare their swimming ability to the flow conditions. If local flow exceeds their capability and their effort is below a defined threshold, they enter STST:

$$|V_{patch}| > V_{agent} \quad \text{and} \quad V_{agent} \leq Speed_{min}$$

While in STST:

Heading aligns with the current (drift vector) & swimming speed is set to:

$$V_{agent} = |V_{patch}|$$

Energy is set as:

$$E_{swim} = swim_{base}$$

Where:

- V_{agent} is the current swimming speed of the agent.
- V_{patch} is the along-channel velocity at the agent's current patch.
- $Speed_{min}$ is the minimum sustainable swimming speed of the agent.
- $swim_{base}$ is the base swimming cost based on agent size.
- E_{swim} is the total energy cost during passive movement.

8.7.2 Behavior During STST

While in STST, agents align with the current (either landward or seaward) and are passively transported:

$$\vec{Y}_{t+1} = \vec{Y}_t + |V_{patch}| \cdot \hat{u}$$

Swimming speed is overwritten:

$$V_{agent} = |V_{patch}|$$

Energy cost is minimized:

$$E_{swim} = swim_{base}$$

Where:

- $\vec{Y}_t$ is the agent's current spatial position.
- $\vec{Y}_{t+1}$ is the position after drifting.
- V_{patch} is the along-channel velocity at the agent's current patch.
- $\hat{u}_{patch}$ is the direction of the patch velocity (unit vector).
- $swim_{base}$ is the base swimming cost based on agent size.
- E_{swim} is the total energy cost during passive movement.

8.7.3 Stop Conditions for STST

Agents exit STST when they regain sufficient swimming capacity to exceed threshold:

$$V_{agent} > Speed_{min}$$

Where:

- V_{agent} is the current swimming speed of the agent.
- $Speed_{min}$ is the minimum sustainable swimming speed of the agent.

This triggers a return to active migratory movement and deactivates $STST_?$.

Chapter 9

Staging Behavior

9.1 Overview

Staging is a behavioral state that allows agents to temporarily halt migration and recover energy or acclimate to dynamic estuary conditions (i.e., temperature, salinity) before continuing upstream (landward) or downstream (seaward) movement. It is triggered when agents experience low energy or high physiological stress and is resolved when recovery thresholds are met.

9.2 Purpose

To simulate the biologically necessary pause in migratory activity used for energy recovery and physiological acclimation, particularly under stressful conditions.

9.3 Entities, State Variables, and Scales

9.3.1 Patch Variables

Variable Name	Definition
Velocity V_{patch}	The along-channel velocity of a given patch, derived from hydrodynamic model inputs, where positive values are in the landward direction and negative values are in the seaward direction.
staging-in-patch	Count of staging agents within a patch (for habitat quality analysis).

9.3.2 Agent Variables

Variable Name	Definition
size M_{agent}	The size of an agent.
M-max M_{max}	Maximum size found within the agent's population.
age A_{agent}	The age of an agent.
A-max A_{max}	Maximum age found within the agent's population.
energy E_{agent}	The total energy the agent currently possesses.
stress S	Stress level based on environmental mismatch.
staging? $stage_?$	Boolean flag indicating whether the agent is currently staging.

9.4 Process Overview and Scheduling

1. Evaluate energy and stress levels.
2. If energy is 25% or stress > 5, agent enters staging behavior.
3. During staging, agents stop migrating, form schools, seek calm water, and regain energy.
4. If energy 75% and stress $= 1$, staging ends and active migration resumes.

9.5 Design Concepts

Basic Principles: Staging is based on physiological ecology principles recognizing the need for energetic and osmoregulatory recovery before continued migration.

Emergence: Collective staging areas and patterns emerge from local environmental conditions and individual agent needs.

Adaptation: Agents adaptively stop migrating when unable to continue due to exhaustion or stress, shifting to a recovery behavior.

Sensing: Agents assess their internal energy and stress state.

Stochasticity: Recovery rate includes random variation to simulate individual differences.

Collectives: Agents may cluster spatially during staging but do not form persistent groups.

Observation: Number of staging agents and energy dynamics can be recorded for habitat analysis.

9.6 Initialization

Variable	Initialized Value	Justification
size M_{agent}	user-defined and species-specific	Representative body length of a migrating agent.
M-max M_{max}	user-defined and species-specific	Based on the maximum body length in the agent's population.
age A_{agent}	user-defined and species-specific	Representative age length of a migrating agent.
A-max A_{max}	user-defined and species-specific	Based on the maximum age in the agent's population.
energy E_{agent}	100%	Agent starts migration at 100% relative energy capacity.
Stress S	1	Acclimated agents have minimal stress levels.
k	0.75	Energetic scaling component that follows Kleiber's Law.
α	-0.3 to 0.5 (user-defined)	This value can be calibrated based on your biological assumptions: • $\alpha < 0$: Younger fish recover faster (higher turnover, rapid metabolism) • $\alpha > 0$: Older fish recover faster (more energy reserves, lower stress sensitivity) • $\alpha = 0$: Age has no effect on recovery (neutral assumption)

9.7 Submodels

9.7.1 Trigger Conditions for Staging

Agents will enter the staging state under either of the following conditions:

$$E_{agent} \leq 25\%$$

$$S > 5$$

Where:

- E_{agent} is the current energy available to the agent.
- S is the current stress level of the agent.

These thresholds are designed to prevent migration collapse due to exhaustion or high osmotic stress.

9.7.2 Behavior During Staging

During staging, agents move to the nearest water patch with the lowest absolute velocity to reduce energetic costs. If no such patch is found, a random neighboring water patch is selected.

Position is updated as:

$$\vec{Y}_{t+1} = \vec{Y}_{target}$$

Energy recovery occurs at a variable rate:

$$E_{agent} = E_{agent} + \left((1+\epsilon) \cdot \left(\frac{M_{agent}}{M_{max}} \right)^k \cdot \left(\frac{A_{agent}}{A_{max}} \right)^\alpha \right) \quad \text{where } \epsilon \sim U(0,1),\ k \leq 1$$

Patch records presence of staging agents:

$$\text{staging-in-patch} = \text{staging-in-patch} + 1$$

Where:

- $\vec{Y}_{t+1}$ is the position after drifting.

- $\vec{Y}_{target}$ is the agent's target spatial position.
- V_{patch} is the along-channel velocity at the agent's current patch.
- M_{agent} is the size of the agent.
- M_{max} is the maximum size within the agent's population.
- A_{agent}: the age of the agent.
- A_{max}: the maximum age within the population.
- E_{swim} is the total energy cost during passive movement.
- k is the scaling exponent, reflecting nonlinear energy recovery.
- α: an age-scaling exponent

Suggestion:

- $\alpha = -0.25$ if modeling faster recovery in younger fish.

- $\alpha = 0.25$ if modeling increased efficiency in older/larger individuals.

9.7.3 Stop Conditions for Staging

Agent will remain in the staging state until both of the following conditions are met:

$$E_{agent} \geq 75\%$$

$$S = 1$$

Where:

- E_{agent} is the current energy available to the agent.
- S is the current stress level of the agent.

Chapter 10

Homing Behavior

10.1 Overview

10.2 Purpose

10.3 Entities, State Variables, and Scales

10.3.1 Patch Variables

Variable Name	Definition

10.3.2 Agent Variables

Variable Name	Definition

10.4 Process Overview and Scheduling

1.
2.
3.
4.

10.5 Design Concepts

Basic Principles:

Emergence:

Adaptation:

Objectives:

Learning:

Prediction:

Sensing:

Interaction:

Stochasticity:

Collectives:

Observation:

10.6 Initialization

Variable	Initialized Value	Justification

10.7 Submodels

Chapter 11

Foraging Behavior

11.1 Overview

Foraging is a facultative behavior triggered under specific physiological and environmental conditions. In this model, fish evaluate nearby patches and opportunistically forage only when their energy is low, stress is minimal, and conditions are suitable. This behavior is designed to simulate optimal foraging theory for migratory fish within a spatially explicit, agent-based framework.

11.2 Purpose and Patterns

The purpose of this submodel is to simulate facultative foraging behavior in migratory fish, where agents opportunistically forage during natural pauses in migration when energy is low but physiological stress is minimal. The behavior is shaped by individual condition, environmental suitability, and competition from other fish. This framework allows the model to assess foraging quality, competition, and the ecological trade-offs fish face during migration.

The following ecological patterns are represented as explicit rules in the model:

- **Conditional foraging triggers**:
  Fish forage only when **all** of the following are true:
  `Staging? = true`, `Energy < 75%`, `Ionregulatory stress < 3`, `Thermal stress < 3`, and `SPM < mean SPM`.
  (Reflects behavioral ecology studies showing fish avoid feeding during stress and turbidity but will opportunistically forage when paused.)
- **Habitat-based foraging selection**:
  Fish score nearby patches based on salinity, temperature, depth, velocity,

and turbidity (SPM), and choose the one with the highest score.
(Represents optimal foraging theory and empirical habitat preference studies in estuarine fish.)

- **Intraspecific competition**:
  Fish can forage alongside others of the same species, but energy gain is reduced when the patch is crowded.
  (Captures resource sharing and diminishing returns observed in schooling behavior.)
- **Interspecific competition**:
  Fish will not forage in patches where larger individuals of a different species are already present. They will search again for the next best patch.
  (Reflects asymmetric, size-structured competition documented in estuarine communities.)
- **Size-based exclusion**:
  Fish avoid patches where the **combined size** of all different-species foragers is greater than their own.
  (Simulates energetic trade-offs in contested foraging zones.)

11.3 Entities, State Variables, and Scales

11.3.1 Patch Variables

Variable Name	Definition
Salinity S_{patch}	The current salinity at the patch location
Temperature T_{patch}	The current temperature at the patch location
Velocity V_{patch}	The along-channel velocity at the patch
Depth d_{patch}	The water depth at the patch
SPM SPM	Suspended particulate matter concentration
Forage Visits $forage-visits$	The number of times a patch has been visited for foraging
Forage Species $forage-species$	List of species that have foraged on this patch
Forager Count $forager-counts$	Number of agents currently foraging on patch

11.3.2 Agent Variables

Variable Name	**Definition**
energy	Current energy level of the agent
foraging?	Boolean indicating if the agent is currently foraging
acclimated-salinity	Current internal salt balance acclimated to
optimal-temperature	Preferred temperature
optimal-depth	Preferred depth
optimal-velocity	Preferred current velocity
ionregulatory-stress	Stress level based on osmoregulatory load
thermal-stress	Stress level based on thermal tolerance
staging?	Boolean for staging behavior
breed	Species classification (used to exclude non-foragers)

11.4 Process Overview and Scheduling

1. Fish evaluate local conditions only when `Staging? = true`, `Energy < 75%`, `Ionregulatory stress < 3`, `Thermal stress < 3`, and `SPM < mean SPM`.
2. The agent assesses neighboring patches for suitability.
3. The best patch is selected only if no larger individual of a different species is already present. If out-competed, the agent will move to the second best patch and try again.
4. Energy gain is scaled down by the number of agents present on that patch.
5. Patch visitation and species are tracked for foraging density and competition analysis.

11.5 Design Concepts

Basic Principles:
Fish only forage during rest periods along their migration route. They do not interrupt active migration solely to seek food. Foraging occurs facultatively when conditions are favorable and the fish have temporary reprieve from other energetically costly behaviors. This reflects optimal foraging theory, where agents balance energy needs with the opportunity to feed without compromising migration.

Emergence:
Spatial foraging hotspots emerge from a combination of individual preferences, environmental suitability, and dynamic competition from other foragers.

Adaptation:
Agents decide whether to forage based on their internal energy level, physiological stress, and the presence of competitors in surrounding patches.

Sensing:
Agents sense local environmental conditions like salinity, temperature, depth, velocity, and SPM, along with, social cues like the size and species of other foragers. They avoid moving into patches occupied by larger fish or where the total biomass exceeds their own size.

Stochasticity:
Foraging success is not deterministic; energy gain includes a random multiplier to account for variability in foraging efficiency and prey availability.

Interaction:
Competition is modeled through species- and size-based exclusion. Agents will not forage in a patch if a larger individual of a different species is already present. However, they may forage alongside larger individuals of their own species. If out-competed, the agent moves to a random neighboring patch. Energy gain is shared among all foragers on the patch, simulating diminishing returns under crowding.

Observation:
The model records foraging events, patch visitation frequency, species identity, and total forager biomass per patch to support analyses of habitat quality and interspecific competition.

11.6 Initialization

Variable	**Initialized Value**	**Justification**
energy	100	Represents full energy at migration onset
foraging?	false	Starts false; updated based on conditions
ionregulatory-stress	1	Minimal stress at initialization
thermal-stress	N/A	Calculated from environmental conditions
forage-visits	0	No patch has been visited at setup
forage-species	empty list	No species recorded at setup
forager-count	0	No agents foraging initially

11.7 Submodels

11.7.1 Trigger Conditions for Foraging

Fish initiate foraging if:

$$staging? = \text{true} \quad \text{and} \quad E_{agent} < 75 \quad \text{and} \quad S_{ion} < 3 \quad \text{and} \quad S_{thermal} < 3 \quad \text{and} \quad SPM < \overline{SPM}$$

- `staging? = true` (i.e., the fish is not actively migrating)
- `energy < 75%` (low energy state)
- `ionregulatory-stress < 3` (low osmoregulatory stress)
- `thermal-stress < 3` (within thermal tolerance)
- `SPM < mean SPM` (low turbidity)

11.7.2 Patch Evaluation

Each agent evaluates neighboring patches for optimal foraging conditions:

$$Score = \left(0.2 \cdot Sal_{opt} + 0.3 \cdot temp_{opt} + 0.2 \cdot vel_{opt} + 0.2 \cdot depth_{opt} + 0.1 \cdot spm_{penalty}\right) \cdot (\text{random}(0, 3.0))$$

Where:

- $sal_{opt} = 1 - \frac{|salinity - acclimated\ salinity|}{10}$
- $temp_{opt} = 1 - \frac{|temperature - optimal\ temperature|}{10}$
- $vel_{opt} = 1 - |velocity - optimal\ velocity|$
- $depth_{opt} = 1 - \frac{|depth - optimal\ depth|}{2.5}$
- $spm_{penalty} = 1 - \frac{SPM - mean\ SPM}{mean\ SPM}$ (bounded to [0,1])

11.7.3 Species and Size-Based Competition Constraints

Agents will only forage in a patch if either (1) the patch is unoccupied, (2) the patch contains only members of the same species, or (3) all other individuals on the patch are smaller if they are of a different species. This behavior simulates asymmetric, size-based competition, where larger individuals of different species out-compete smaller fish for access to high-quality foraging habitat.

Then foraging is allowed only if:

$$b_{\text{agent}} \in \mathcal{B}_{\text{others}} \quad \text{or} \quad \left(S_{\text{sum}} < S_{\text{agent}} \text{ and } b_{\text{agent}} \notin \mathcal{B}_{\text{others}}\right)$$

Where:

- S_{agent}: size of the focal fish
- $S_{\text{sum}} = \sum_i S_{\text{agent}_{b_{\text{others}}\, i}}$
- b_{others}: set of breeds (species) of other foragers on the patch
- b_{agent}: the breed of the focal fish

If a patch is occupied by a larger fish of a different species, the agent is considered out-competed and will seek the next most suitable patch among its neighbors. This ensures that foraging attempts are adaptive to interspecific competition.

11.7.4 Energy Gain

Energy gain is then calculated:

$$E_{\text{gain}} = \left(\frac{\text{Score}_i}{\sum_{j=1}^{N} size_j}\right) \cdot size_i$$

Where:

- $Score_i$ is the individual fish's foraging score (bounded between 0 and 3)
- $Size_j$ is the sum of sizes for all N foraging fish on that patch
- $\sum_{j=1}^{N} size_j$ is the sum of sizes for all N foraging fish on that patch

11.7.5 Foraging Patch Tracking

Each time a fish forages on a patch, the following patch-level variables are updated:

- `forage-visits`: Increments by 1 with each foraging event, enabling spatial analysis of foraging intensity.
- `forager-count`: Tracks the number of agents currently foraging on the patch, reflecting competition density.
- `forage-species`: Stores a list of species that have foraged on the patch, supporting interspecific competition analysis.

Chapter 12

Predation and Fleeing Behavior

12.1 Overview

This module simulates predator–prey interactions between migratory fish species, specifically predators (i.e., striped bass) and prey (i.e., alewife), during key migratory and staging periods. Predators detect, pursue, and consume prey based on visibility conditions and prey size constraints. Prey detect approaching predators through visual and social cues and respond with directional fleeing behaviors, which vary based on their size, age, energy level, and water clarity. These behaviors reflect biologically observed trade-offs between escape speed, reaction time, and group-based vigilance. The model also tracks predator energy gain and prey energy depletion and recovery, allowing for analysis of individual fitness and risk exposure under different environmental and behavioral conditions.

12.2 Purpose and Patterns

This submodel captures ecologically grounded predator–prey dynamics by simulating behaviorally realistic rules of pursuit and evasion observed in estuarine fishes.

- Prey initiate fleeing based on predator proximity, visual detection, and turbidity-adjusted reaction time, reflecting sensory limitations in murky estuarine water.

- Predators only pursue prey that are within their gape limit and provide a favorable energy return, consistent with optimal foraging theory and size-selective predation.
- Fleeing speed is scaled by energy and body size, capturing the biologically observed trade-off between fatigue and escape performance.
- Directional fleeing (left, right, up, or down) is based on the predator's relative position, aligning with empirical studies on spatial escape responses.
- Patch-level alarm cues propagate fleeing behavior across prey groups, mimicking the benefits of schooling and collective vigilance in fish.
- Energetic constraints influence both predator foraging frequency and prey escape success, contributing to variability in encounter outcomes.
- Spatial tracking of predation events allows identification of high-risk zones, offering insight into how environmental conditions shape survival landscapes.

12.3 Entities, State Variables, and Scales

12.3.1 Spatial and Temporal Scales

- **Spatial Unit**: Patch (3 m x 3 m resolution)
- **Temporal Unit**: 5-minute time steps (`tick`)

12.3.2 Patch Variables

Variable Name	Definition
Suspended-particulate-matter SPM_t	Level of suspended material in patch (exponential difficulty increase between min and max observed in system) worse vision at max, best vision at min
Prey-Eaten-in-Patch	Counts how much prey are consumed in a patch
Prey-in-Patch $prey-in-patch_t$	The amount of prey currently in the patch
prey-alarmed?	Boolean variable set to true if any prey in the patch initiates fleeing behavior, triggering collective escape.

12.3.3 Prey: Agent Variables

Variable Name	Definition
vision	Radius (in patches) within which the prey can detect predators. Decreases with high SPM.
fleeing?	Boolean indicator of whether the prey is actively escaping from a predator.
energy	Energy levels of an agent
swimming speed	The speed at which a prey agent is moving
max-speed	Maximum normal swim speed (not in a flee state).
max-flee	Maximum achievable fleeing speed, calculated as a function of max-speed, swimming-speed, size, and max-rate-of-speed-change.
reaction-time	Time delay in response to predator presence. Increases with smaller size, higher SPM, larger/faster predators, and lower flee-ability.
size	Body length (size) of the prey; influences visibility and escape ability.
age	Agent's age class; mid-range age groups tend to have better escape success (a normal distribution across age classes).
flee-ability	Learning metric based on age; moderate-aged fish have best reflexes and performance.

12.3.4 Predator: Agent Variables

Variable Name	Definition
vision	Radius (in patches) within which predator can visually detect prey. Decreases with high SPM or low prey size.
swimming-speed	The speed at which a predator agent is moving
max-speed	Maximum normal swim speed (not in a burst state).

Variable Name	Definition
bursting?	Boolean indicating whether the predator is currently in a high-speed chase or attack behavior.
prey-in-vision	Agentset of prey within vision range
daytime-prey-eaten	Count of prey eaten that day
time-since-full	Time since last feeding (when will predator be hungry again?)
reaction-time	Delay between prey detection and initiation of chase. Influenced by predator size/age, prey density, prey speed, water clarity (SPM), and predation ability.
limit-daily-prey-allowance	Max prey allowed per day (predator becomes full)
gape-limit	Maximum size of prey the predator can successfully capture and ingest.
handling-effort	Time and energy cost required to subdue and consume a prey item. Depends on distance, prey size, and prey density. Used in patch and prey selection decisions.
size	Body length (size) of the prey; influences visibility and escape ability.
age	Age class of the predator agent. Predation success follows a normal distribution across age classes.
predation-ability	Agent's age class; mid-range age groups tend to have better predation success (a normal distribution across age classes).
prey-species-eaten	Species identifiers of consumed prey; enables diet tracking and multispecies modeling.
total-prey-eaten	Cumulative prey consumed across all days or scenarios.
digestion-time	Time it takes to digest prey

12.4 Process Overview and Scheduling

12.4.1 Prey Behavior (per agent)

1. **Fleeing Trigger**
   Each prey evaluates whether a predator is in its visual cone or whether `prey-alarmed? = true` in the patch. If so, the prey calculates reaction time based on its own size, age, flee-ability, local SPM, and the predator's size and speed.
2. **Directional Escape**
   If the reaction time threshold is met, the prey executes a directional fleeing behavior (`scare-left`, `scare-right`, `scare-down`, or `scare-up`), and sets the patch to `prey-alarmed? = true`.
3. **Schooling Response**
   All other prey in the same patch automatically begin fleeing when `prey-alarmed? = true`, simulating social alarm propagation.
4. **Speed and Energy Update**
   If the agent is fleeing, its speed increases toward `max-flee`, and energy is reduced based on movement cost. If not fleeing, the agent moves normally and may recover energy depending on its resting status.

12.4.2 Predator Behavior (per agent)

1. **Visual Detection**
   The predator identifies prey within its in-cone vision, adjusted based on local SPM concentration, prey size, and predator size.
2. **Prey Filtering**
   Prey that exceed the predator's gape limit or whose handling effort exceeds the predator's available energy are excluded.
3. **Prey Selection**
   Among remaining prey, the predator evaluates candidates using an optimal foraging approach that considers size, handling effort, and net energy gain. One prey is selected.
4. **Pursuit Decision**
   If a prey is selected, the predator enters a bursting state, increasing its speed toward max-speed. Reaction time is computed based on predator age, size, SPM, and prey proximity.
5. **Scare Prey**
   The predator triggers fleeing in visible prey by calling the `scare-prey` procedure. If any prey flees, the patch is flagged as `prey-alarmed? = true`.

6. **Consume Prey**
   If within striking range, the predator consumes the prey and updates variables: `daytime-prey-eaten`, `prey-species-eaten`, `total-prey-eaten`, and `Prey-Eaten-in-Patch`.

7. **Digestion**
   If no prey are eaten, `time-since-eaten` increases. If the predator has reached its daily feeding limit, it enters a digestive phase. Digestion ends when both `time-since-eaten` and `time-since-full` exceed the digestion time

12.5 Design Concepts

Basic Principles: Simulates predator and prey interactions in a spatial estuarine system. Behaviors such as chasing, fleeing, and feeding are determined by individual traits, patch conditions, and environmental clarity due to suspended particulate matter.

Emergence: Predation hotspots develop in areas with higher prey density and better visibility. Prey movement and group alarm responses create shifting patterns of refuge and risk across the landscape.

Adaptation: Prey modify their direction and intensity of escape based on the predator's location and their own size, age, and escape ability. Predators filter out prey that are too large to consume and shift to resting behavior after reaching their feeding limit.

Objectives: Predators aim to select prey that provide the highest net energy gain while minimizing pursuit and handling costs. Prey aim to avoid detection or flee successfully using both individual detection and social alarm cues.

Learning: Learning is represented through Mid-aged agents generally perform better than very young or very old individuals.

Prediction:

Sensing: Agents rely on in-radius and in-cone vision to detect others. Detection range is influenced by water clarity, body size, and prey movement. Predators exclude prey that are too large to handle even if they fall within the visible field.

Interaction: Predators and prey interact through visual detection, spatial proximity, and energy transfer through feeding. Social interactions occur through alarm cue propagation at the patch level and school level.

Stochasticity: Prey selection, fleeing direction, and reaction timing include probabilistic variation. Randomness is used to reflect natural variability in movement and perception.

Collectives: When one prey detects a predator and flees, all prey in the same patch respond. This collective behavior improves predator detection and increases the likelihood of survival through schooling.

Observation: Key outputs include prey consumption, alarm responses, spatial predation distribution, and energy use of individual agents.

12.6 Initialization

Variable	Initialized Value	Justification
energy	100	Prey begin fully energized to allow immediate fleeing or normal movement
fleeing?	false	Prey are not actively escaping at the start
prey-alarmed?	false	Alarm cue inactive at start of simulation
daytime-prey-eaten	0	daily counter of prey eaten starts at zero
time-since-full	0	predator begins simulation hungry
gape-limit	function of size	Large predators have wider gape limits
handling-effort	calculated per encounter	Depends on prey traits and local patch conditions
reaction-time	size-, age-, and SPM-based	Prey and predator values dynamically computed each tick
flee-ability	based on age	Represents individual escape competence across age classes
predation-ability	based on age	Mid-age predators have fastest and most accurate prey responses
max-speed	1.5-3.0x size	

12.7 Submodels

12.7.1 Prey Detection Probability

Visual detection of prey by predators is scaled by local water clarity, prey size, and prey movement. The effective detection radius decreases as SPM increases and increases as prey size increases.

$$P_{detect} = \left(\frac{S_{prey}}{S_{max}}\right) \cdot e^{-SPM_t/\tau}$$

Where:

- P_{detect} is the probability of detecting a prey agent.
- S_{prey} is the size of the prey agent.
- S_{max} is the maximum size of any prey in the system.
- SPM_t is the suspended particulate matter concentration in the current patch.
- τ is a turbidity scaling constant.

Biological Justification: Larger prey are more visible, but high turbidity (SPM) reduces contrast and visual range. The exponential function reflects rapid degradation of visibility with increased turbidity.

12.7.2 Reaction Time

Reaction time determines how quickly an agent initiates a behavior in response to a threat (for prey) or opportunity (for predators). It is influenced by SPM, size, age, and ability.

$$RT_{agent} = \left(\frac{1}{F_{ability}} \cdot \frac{S_{opp}}{S_{agent}}\right) \cdot (1 + \alpha \cdot SPM_t)$$

Where:

- RT_{agent} is the reaction time of the prey or predator.
- $F_{ability}$ is flee-ability (for prey) or predation-ability (for predators).
- S_{opp} is the size of the opposing agent (predator or prey).

- S_{agent} is the size of the focal agent.
- SPM_t is the suspended particulate matter in the patch.
- α is the turbidity penalty factor.

Biological Justification: Smaller or younger fish tend to react slower. High turbidity delays response time. Age-related ability improves reaction time in middle-aged agents.

12.7.3 Alarm Response Propagation

$$P_{alarm} = 1 - e^{\frac{-n_{flex}}{k}}$$

Where:

- P_{alarm} is the probability that non-detecting prey will flee.
- n_{flee} is the number of fleeing fish in the patch.
- κ is a sensitivity constant governing social responsiveness.

Biological Justification: Prey benefit from collective vigilance. The more individuals that flee in a patch, the more likely others will follow.

12.7.4 Fleeing Speed

The maximum speed a prey agent can reach when fleeing is scaled by body size, energy, and physical acceleration limits.

$$V_{flee} = V_{max} \cdot \left(\frac{E_{agent}}{100} \right) + \delta \cdot S_{agent}$$

Where:

- V_{flee} is the maximum fleeing speed.
- V_{max} is the prey's maximum speed.
- E_{agent} is the energy level of the prey agent.
- S_{agent} is the size of the prey.
- δ is a scaling factor for size-based speed increase.

Biological Justification: Larger prey generally swim faster, but energy limits how much of that speed can be used. Exhausted fish flee more slowly.

12.7.5 Handling Effort

Predators calculate the cost of pursuing and consuming prey using the prey's size and density, and the distance to the target.

$$H_{effort} = \gamma \cdot S_{prey} \cdot D_{patch} \cdot \left(1 + \frac{1}{\rho_{patch}}\right)$$

Where:

- H_{effort} is the handling effort for the predator.
- S_{prey} is the size of the prey.
- D_{patch} is the distance between predator and prey.
- ρ_{patch} is the prey density in the patch.
- γ is a handling cost coefficient.

Biological Justification: Prey that are farther away or more dispersed are harder to catch. Denser prey clusters reduce handling time by enabling rapid repeat captures.

12.7.6 Gape Filtering

Predators apply a binary filter before pursuit, excluding prey that exceed their maximum ingestible size.

$$P_{pursue} = \begin{cases} 1 & \text{if } S_{prey} \leq G_{pred} \\ 0 & \text{otherwise} \end{cases}$$

Where:

- P_{pursue} is the pursuit decision (1 = pursue, 0 = ignore).
- S_{prey} is the size of the prey.
- G_{pred} is the predator's gape limit.

Biological Justification: Predators cannot capture or ingest prey that are too large, so these individuals are ignored even if they are detected.

12.7.7 Energy Gain by Predators

$$E_{agent} = E_{agent} - E_{burst}$$

Where:

- E_{agent} is the current energy of the predator.
- E_{burst} is the energy cost per unit of bursting behavior.

Biological Justification: Bursting reduces available energy. Energy cost is a limiting factor for predation.

12.7.8 Energy Depletion by Prey

$$E_{agent} = E_{agent} - E_{flee}$$

Where:

- E_{agent} is the current energy of the prey.
- E_{flee} is the energy cost per unit of fleeing behavior.

Biological Justification: Fleeing reduces available energy and increases recovery time. Energy loss is a limiting factor for repeated escape attempts.

(no need to account for swimming energy in addition if you are using the migration functions)

Chapter 13

Spawning Behavior

13.1 Overview

This submodel simulates the conditions, triggers, and behavioral outcomes associated with spawning in anadromous fish. It integrates physiological thresholds, habitat preferences, reproductive strategies, and energy-based constraints to identify spawning events and their consequences during migration.

13.2 Purpose and Patterns

This submodel captures ecologically grounded reproductive strategies in anadromous fishes by simulating individual-based spawning behavior as a function of habitat, physiological readiness, and reproductive strategy.

- Spawning is initiated when agents meet combined salinity and thermal stress thresholds and have sufficient energy reserves, reflecting empirically observed constraints on reproductive viability in migratory fishes.
- Broadcast spawners initiate spawning in freshwater patches with suitable depth and flow conditions, consistent with the behavior of species like alewife and rainbow smelt. Fertilization success is probabilistically scaled by the local density of mature males, reflecting external gamete mixing dynamics in flowing water.
- Pairwise spawners, such as sturgeon and striped bass, require physical co-location of a reproductively ready male and female in suitable habitat. This reflects species that engage in close-contact courtship and synchronize gamete release based on microhabitat cues.

- Spawning events result in an immediate energy cost and update internal states for both male and female agents. Iteroparous species may spawn more than once if conditions remain favorable, while semelparous species are subject to mortality following reproductive exhaustion.
- Energetic depletion after spawning triggers resting or staging behavior before resuming seaward migration. Overwintering probability is dynamically calculated based on energy levels, spawning timing, age, and size, reflecting seasonal decisions observed in species like Atlantic salmon and shortnose sturgeon.
- Spatial overlap of spawning-ready agents in high-quality patches allows emergent identification of reproductive hotspots and helps model the intersection of life history traits and estuarine hydrodynamics.

13.3 Entities, State Variables, and Scales

13.3.1 Spatial and Temporal Scales

- **Spatial Unit**: Patch (3 m x 3 m resolution)
- **Temporal Unit**: 5-minute time steps (`tick`)

13.3.2 Patch Variables

Variable Name	Definition
Salinity S_{patch}	anadromous fish are known to typically spawn in freshwater reaches of the estuary
Temperature T_{patch}	Patch-level temperature from hydrodynamic model
Depth d_{patch}	Patch-level water column depth
Velocity V_{patch}	Patch-level water velocity
spawning-in-patch	Boolean flag indicating active spawning event

13.3.3 Agent Variables

Variable Name	Definition
size M_{agent}	Individual fish body size
age A_{agent}	Individual fish age

Variable Name	Definition
sex s_{agent}	Sex of agent
energy E_{agent}	Current metabolic energy level
spawning energy E_{spawn}	Energy cost to spawn
spawning encounters $spawn_{encounters}$	Count of fertilization events related to agent's spawn
spawns $spawn_n$	Number of individual spawning encounters
spawning limit lim_{spawn}	Maximum spawns allowed for individual
spawning strategy	Reproductive mode (broadcast or pairwise)
Salinity Stress S_{stress}	Osmotic stress response
Thermal Stress T_{stress}	Deviation from thermal optima
Staging?	Boolean for if fish is staging
STST?	Boolean for if agent is using Selective Tidal Stream Transport

13.4 Process Overview and Scheduling

1. **Spawning Readiness**
   Each agent evaluates whether it is spawning-ready based on salinity stress, thermal stress, energy levels, and whether it has exceeded its spawning limit. If all conditions are met, the agent is considered ready to spawn.

2. **Spawning Strategy**
   For broadcast spawners, the female initiates spawning if the patch meets the suitability criteria. Fertilization probability is calculated based on the number of males within the local radius. For pairwise spawners, spawning occurs only if one male and one female are both in the same patch, both are spawning-ready, and habitat conditions meet the required criteria.

3. **Spawning Energy**
   After spawning, the agent's energy is reduced by the spawning energy cost.

4. **Post-Spawning Behavior**
   If the agent's energy is sufficient, it switches to seaward migration. If energy is below the threshold, the agent enters a resting/staging state until its energy is restored.

5. **Mortality Risk**
   For semelparous species, the mortality risk increases after spawning, with the probability increasing based on age. For iteroparous species, the mortality risk is lower and also age-dependent.

6. **Overwintering Probability**
   The overwintering probability is calculated based on the agent's energy, age, size, and days since the last spawning. Overwintering is more likely for older fish, those with low energy, or those that spawned recently.

13.5 Design Concepts

Basic Principles: Spawning behavior in anadromous fish is influenced by a combination of environmental conditions (salinity, temperature, depth, and velocity) and physiological readiness. Fish assess these conditions and their internal energy reserves to decide when and where to spawn.

Emergence: High-quality spawning patches with favorable environmental conditions emerge, and spawning encounters increase in these areas. Overlap of spawning-ready agents in these patches leads to emergent patterns of reproductive success.

Adaptation: Fish respond to varying environmental conditions by adjusting their spawning behavior. Broadcast spawners will select the highest probability patch based on the presence of males, while pairwise spawners rely on physical proximity for spawning. Iteroparous species may spawn multiple times in a season if conditions remain favorable, whereas semelparous species spawn once and die.

Objectives: The primary objective of spawning behavior is to maximize reproductive success. This is achieved by ensuring optimal environmental conditions for gamete fertilization while minimizing the energetic cost of spawning and migration.

Prediction: Broadcast spawners do not predict future conditions but react to local male density and environmental suitability. Pairwise spawners predict spawning success based on habitat conditions and the availability of a mate.

Sensing: Agents sense local patch temperature, salinity, depth, and velocity. They also assess the presence of other agents (both male and female) to determine readiness for spawning.

Interaction: Male and female agents interact through proximity in pairwise spawning, while broadcast spawners interact with males via fertilization probability calculations. Both strategies involve the exchange of gametes, with varying degrees of synchronization and spatial organization.

Stochasticity: The model includes probabilistic factors in fertilization success and mortality. For broadcast spawners, fertilization success is probabilistically scaled by the number of males, while mortality is age-dependent.

Observation: The model tracks spawning encounters, spawning energy expenditures, energy recovery, mortality rates, and overwintering probabilities.

13.6 Initialization

Variable	Initialized Value	Justification
E_{agent}	100	Assumes full energy at initialization
E_{spawn}	species-specific	Threshold to permit spawning
$spawned-this-tick?$	false	Agent has not spawned yet
A_{agent}	population distribution	Age assigned from population parameters
M_{agent}	size-at-age curve	Species-specific size growth
$spawning-strategy$	broadcast or pairwise	Species-level trait
lim_{spawn}	dependent on sex and species	How many times a fish is capable of spawning in a single migration
S_{stress}	0	No stress at initialization
T_{stress}	0	No stress at initialization
$S_{overwinter}$	0 or 1	Binary species trait
t_{spawn}	0	Time since last spawning
$E_{recover}$	75	Required energy to resume post-spawning migration

13.7 Submodels

13.7.1 Spawning Readiness

Agents are considered spawning-ready if they meet the following conditions:

$$\text{SpawningReady} = \begin{cases} \text{true}, & \text{if } S_{stress} < 3 \text{ and } T_{stress} < 3 \text{ and } E_{agent} > E_{spawn} \text{ and } spawn_n < lim_{spawn} \\ \text{false}, & \text{otherwise} \end{cases}$$

- S_{stress} = salinity stress
- T_{stress} = thermal stress
- E_{agent} = current energy level of agent
- E_{spawn} = minimum energy required for spawning (species-specific)
- $spawn_n$ how many spawns agent has performed

13.7.2 Spawning Strategy

13.7.2.0.1 If `spawning-strategy = broadcast`:

1. Female agent initiates spawning if the patch meets habitat criteria.
   - $S_{patch} <= 0.5$
   - $d_{patch} <= 3$
   - $staging? = false$
   - $STST? = false$
2. The agent evaluates **neighboring patches** for the **fertilization probability** ($P_{fertilize}$) sexually mature males in the local radius (n_{males}).

The fertilization probability is calculated as:

$$P_{fertilize} = 1 - e^{-\alpha \cdot n_{males}}$$

Where:

- $P_{fertilize}$ fertilization success probability
- α = proximity sensitivity constant
- n_{males} = number of sexually mature males within a defined radius

If no suitable patch with $P_{fertilize} > 0.5$ is found, the female moves to the next patch and repeats the evaluation process until a suitable patch is identified.

Alternatively, if the female encounters a male in the same patch, the fertilization probability is considered high (near 1), and the female spawns immediately without evaluating neighboring patches.

Spawning encounters are recorded as:

$$spawn_n = spawn_n + 1$$

$$Spawn_{encounters} = \sum_{i=1}^{N_f} P_{fertilize,i}$$

Where:

- $spawn_{encounters}$ is the number of spawning encounters
- $P_{fertilize}$ is the probability of fertilization.
- N_f is the number of spawning-ready females in suitable patches.