

# GoFish: A Next-Generation ToolKit for Modeling Migratory Fish and Quantifying 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 modeling, while supporting the empirical quantification of ecological relationships that influence movement, survival, and habitat use of migratory fish.

## 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).

## **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 **man.vanessa98@gmail.com**.

# Chapter 1

## Introduction

Anadromous fish species such as river herring, striped bass, salmon, 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.

As a result, traditional approaches to simulating anadromous fish frequently oversimplify or exclude key biological functions and environmental interactions such as salinity exposure and contaminant exposure. Existing models also lack standardized representations of these behaviors and interactions, 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 migratory 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.

### 1.1 Structure

Each chapter in this library corresponds to a major behavior, physiological function, or foundational component relevant to migratory fish, beginning with:

- Co-Development of Agent-Based Models
- Calculate Metabolism
- Salinity Exposure
- Temperature Exposure
- Contaminant Exposure
- Digestion
- Filter Feeding
- Lipid Catabolism
- Landward Migration
- Seaward Migration
- Schooling
- Selective Tidal Stream Transport
- Predator-prey interactions

The final chapters provide 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 (???). 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.

# Chapter 2

## Agent-Based Models

Agent-based models (ABMs) simulate the behavior of individual organisms—called “agents”—and how their interactions with each other and with their environment create larger-scale patterns. Each agent follows a set of simple rules based on physiology, behavior, or environmental cues. When many agents follow these rules simultaneously, complex system-level outcomes emerge, such as migration pathways, schooling patterns, habitat bottlenecks, or exposure hotspots. ABMs are especially useful for ecological systems because they allow researchers and communities to explore how individual decisions scale up to influence population dynamics, habitat use, and risk in changing environments.

ABMs are designed to capture processes that depend on **behavior**, **timing**, **environmental variability**, and **individual differences**. They allow modelers to explore how organisms respond to their surroundings, make movement decisions, and interact with other individuals or species. Because agents experience the environment at fine spatial and temporal scales, ABMs can reveal patterns that occur only when many individuals interact across a dynamic landscape.

### 2.0.1 What ABMs Can Help Us Understand

ABMs can answer questions related to:

- How individual movement decisions accumulate into migration routes or staging locations
- When and where organisms are most exposed to environmental risks
- How behaviors such as foraging, schooling, predator avoidance, resting, or spawning influence exposure or survival

- How variation in traits (size, energy, age, or species) contributes to different outcomes
- How environmental conditions shape habitat use, movement choices, or interactions between species
- How system-level patterns emerge from local behaviors and simple rules
- How alternative conditions or restoration actions might alter movement, habitat use, or exposure

These models are especially useful when management questions depend on **patterns created by individual behavior**, rather than population totals alone.

### 2.0.2 What ABMs Are Not Designed to Do

ABMs cannot provide or replace:

- Exact estimates of population abundance
- Precise contaminant concentrations inside individual organisms
- Direct measurements of chemical or physiological processes
- Predictions of exact numbers of predation or spawning events
- Large-scale demographic projections without additional modeling components
- Replacements for field sampling, monitoring programs, or laboratory measurements

Instead, ABMs offer **process-based insight**, showing how behavior and environmental conditions interact to create observable patterns.

### 2.0.3 Emergent Behaviors

Emergent behavior refers to patterns that arise when many individual agents follow their own rules, creating outcomes that cannot be predicted from observing a single fish on its own. These outcomes develop only when many individuals interact with each other and respond to their surrounding environment at the same time. Many ecological processes such as migration timing, habitat bottlenecks, exposure hotspots, schooling dynamics, predator and prey encounters, and shifts in group structure are emergent rather than linear. They form through small, individual decisions that accumulate into larger and sometimes unexpected system-level patterns.

By visualizing and simulating emergence, ABMs make it possible to see how these individual behaviors scale up to influence population level outcomes and habitat use patterns. This helps identify the specific conditions, behaviors, and locations that shape system-wide responses. For management, this is valuable because it shows how small-scale decisions made by individual fish can contribute to broader patterns that influence risk, habitat quality, restoration effectiveness, management actions, and ecological resilience. Understanding emergence allows managers and communities to explore why certain patterns occur, identify potential leverage points, and anticipate how changes in environmental conditions may alter system behavior in the future.



# Chapter 3

## Co-Development of ABMs: Penobscot Estuary Community Workshop August 6, 2025

This page documents how a participatory workshop informed the functions within this coding library, the representation of physiological processes, behaviors of migratory fish, and their interactions within an estuary. The purpose of this page is to showcase the value added by co-development and increase transparency about the development of this coding library.

The Penobscot Estuary Community Modeling Workshop was designed from the beginning as a co-development space for an agent based model to address mercury toxicity dynamics of anadromous fish within the estuary. The day invited Tribal collaborators, community members, managers, and researchers to shape the modeling objectives, including which species, processes, behaviors, and outputs the model should represent, and how those outputs should be represented in relation to contaminant exposure in the Penobscot River Estuary.

### 3.1 Core Co-Development Themes

Several themes guided the design of the workshop and the way it connects to model development.

- **Shared problem framing.** The workshop centered a shared concern about mercury contamination in the Penobscot River and its effects on

sea-run fish, subsistence access, and recreation use, rather than starting from a predefined modeling objective.

- **Attention to both internal and external processes.** Breakout discussions were split into two rounds, one for “internal” or biological functions of fish such as osmoregulation, thermoregulation, bioaccumulation, and resting, and the second round focused on “external processes” or external interactions with intra- or interspecific factors and environmental responses such as swimming, predation, foraging, and spawning. This structure maps directly onto modules detailed within this library.
- **Participant driven priorities.** Participants were asked which species were most important to understand for management of the system or species that should be prioritized based on community interest, which functions and interactions they believed to be relevant for understanding mercury toxicity in migratory fish, and how those behaviors should be represented.
- **Outputs that answer real questions.** Each participant had the opportunity to propose a question or hypothesis to test using the developed functions and select preferred outputs from the functions such as migration paths, exposure metrics, or habitat use. These wish-list requests now correspond to specific model output routines and visualizations.
- **Accessible language and shared vocabulary.** A glossary of terms translated physiological, hydrodynamic, and modeling concepts into accessible language. This glossary can be found at the end of this document and is intended to support a range of readers.
- **Iterative relationships, not a single event.** The workshop was framed as one step in an ongoing partnership. Feedback forms, follow-up contact options, and explicit invitations for later review are built into the process.

## 3.2 Workshop Development

### 3.2.1 Pre-Workshop Collaboration Steps

Planning the workshop involved months of coordination with partners, including the Penobscot Nation, faculty and staff at the University of Maine, and federal collaborators. The planning process itself was a first stage of co-development.

Key steps included:

- **Clarifying objectives with partners.** Early conversations identified contamination in the Penobscot River, migratory fish, and access to safe subsistence resources as the shared focus. Partners helped guide agenda

development, identify potential participants of interest, and identify community outputs of interest to support Tribal management. Their suggestions were used when conducting outreach.

- **Aligning model scope with community priorities.** The agenda was constructed so that introductory talks on Penobscot Nation natural resource management and contaminants of interest, an overview of estuary dynamics (connection of fish + physical processes + contamination), and an introduction to agent based modeling were followed by interactive surveys and break-out discussions. This allowed participants to identify anadromous species, behaviors, and processes of interest, which then feed directly into the model design.
- **Preparing interactive polls and prompts.** A Mentimeter survey was developed to help participants identify priority species, important environmental drivers, and fish behaviors that shape exposure. These questions now map to the list of behaviors and parameters implemented in the model.

#### Question Example

- **Designing materials for many kinds of learners.** Each participant received a notepad and workshop folder, which included a plain-language glossary, a participant agenda, a hypothesis and output worksheet, and a feedback form. These materials supported participants who learn best through reading, writing, discussion, or visual exploration. Break-out discussions were accompanied by visual demonstrations of function demos, allowing participants to directly address draft model functions for each behavior.

Find examples below.

Note: these are presentations of functions before participant feedback. Updated functions in this library reflect changes informed by the workshop.

### 3.2.2 Identifying Participants of Interest

Participant selection was guided by the goal of gathering diverse knowledge about the river and its fish.

- **Tribal Collaborators.** Representatives from the Penobscot Nation were invited to collaborate because the Penobscot River Estuary is the Ancestral Homeland of the Penobscot Nation and other Wabanaki Peoples. It was necessary to prioritize their concerns and support their management. We wanted to give them a platform to share their work and management

perspectives on migratory fish and contamination. Indigenous people have sovereign rights to migratory species, which have been deeply impacted by contamination in the estuary.

- **Community Experts.** The workshop brought in local managers, fishermen, researchers, engineers, and students whose work focuses on estuarine dynamics, fisheries, remediation, and environmental management in the Penobscot, or who focus on anadromous fish.

### 3.2.3 Enticing Participants to Attend

The invitations and overview materials emphasized that this was a hands-on, collaborative event where participant input would shape real model structure and outputs—not a passive lecture.

Copy of Invitation

Strategies included:

- **Clear framing.** The overview highlighted how tidal dynamics, fish behavior, and mercury contamination intersect in the Penobscot River, and described specific opportunities for participants to contribute knowledge during breakout sessions and wish-list activities. The invitation also emphasized that participants did not need any modeling experience—only their expertise and perspectives.
- **Concrete outcomes.** Participants could request a specific model output or test a hypothesis relevant to their interests, with results attempted to be shared after the workshop (as feasible within model limitations).
- **Relationship building.** The agenda previewed time for partnership discussions, highlighting opportunities to support Tribal priorities and future collaboration on management and research questions.

### 3.2.4 Selecting the Venue

The workshop was held at the Innovation Media Research Center at the University of Maine, a space that could support immersive presentations and movement between small and large group activities.

The venue allowed for:

- **A theater-style room with a large screen.** The introductory talks and interactive survey used a dark background, low lighting, and a large screen to create an immersive experience similar to an intimate concert hall, while still leaving space for questions and discussion.

- **A separate interactive space.** Round tables, easel pads, printed handouts, and discussion areas were set up in a second room for the world-café breakout sessions, allowing participants to interact and face one another in a conversation-style setting as they discussed each function.

### 3.3 Facilitating the Workshop

#### 3.3.1 Agenda Activities

The agenda combined presentations, interactive polls, world-café discussions, and reflection.

Key components included:

- **Welcome, blessing, and introductions.** The day opened with a welcome and words from the Penobscot Nation, followed by introductions and an icebreaker activity asking participants why they attended and what they hoped to gain.
- **Map-based activities.** Participants could pin locations on a system-scale map, connecting their lived experience and knowledge to specific reaches of the river and estuary. This place-based interaction showcased lived knowledge and gave participants autonomy over the spatial representation of the system.
- **Penobscot Nation history and river overview.** A management representative of the Penobscot Nation, Dan Kircheis, provided management context for contaminants and migratory fish, grounding the model in current work conducted within the system.
- **Modeling overview and agent based model presentation.** Modeling presentations introduced the Penobscot system, key hydrodynamic and contaminant processes, and the rationale for an agent based approach. Examples of emergent behaviors and validation were shown on a large screen to make model dynamics visible and engaging.
- **Mentimeter priority setting.** Participants completed an interactive survey about priority species, important environmental drivers, and key behaviors. These responses were summarized live and used to frame the breakout sessions.
- **World café on internal fish processes.** Small rotating groups discussed processes such as osmoregulation, thermoregulation, bioaccumulation, and resting. Discussion leaders presented demos and recorded notes, which later informed how these processes are parameterized and sequenced within this library.

- **World café on external behaviors and conditions.** A second set of rotations focused on external functions such as foraging, migration, predation, and spawning. These conversations helped identify how fish interact with their environment and where and when the model should track exposure risk.
- **Wish list outputs.** Participants wrote down specific outputs they wanted from the model and the reasoning behind each request, including migration timing, exposure patterns, energy budgets, and habitat use. The goal is to incorporate as many of these outputs as possible to support subsequent management and research.

#### Hypothesis Form

- **Model demo.** A short demonstration of the model interface supported visual learners and connected the function modules to emergent behaviors.
- **Partnership and next steps discussion.** The workshop closed with a short session on building partnerships and identifying community projects where the model could support ongoing work. This included relationship-building between participants and completion of a follow-up survey.

#### Participant Survey

- **Facilitation.** Facilitation roles were shared across a team of organizers and volunteers who kept time, prompted discussion, recorded notes, and supported logistics, which allowed the lead modeler to focus on listening and translating insights into model design.

## 3.4 After the Workshop

### 3.4.1 Incorporating Feedback

Immediately following the workshop, participants were invited to fill out feedback forms on what they found most useful, what felt unclear or missing, and how future workshops or model development activities could be improved.

Feedback is being used to:

- Refine explanations of agent based modeling and estuarine processes in the model interface and supporting documents, using more examples, more visuals, and clearer connections between field observations and model rules.
- Adjust the balance between presentation time and discussion time.

- Clarify how participant input has been integrated, so that people can see their contributions in the model structure and outputs rather than only in summary notes.

### 3.4.2 Post-Workshop Follow-Up

Several tools support ongoing co-development after the workshop day itself. This work is still ongoing as products are completed and co-development of final materials continues.

- **Hypothesis and output forms.** The participant hypothesis and output form captured individual questions, preferred outputs, and desired scenarios. These forms now guide scenario design and output routines in the model (as much as feasible within model limitations and scope), and follow-up emails will share results with those who opted in.
- **Ongoing communication.** Participants who requested follow-up are being contacted with model updates, refinements, and opportunities to review model structure.
- **Follow-up survey.** The feedback form includes an option to receive a later survey on model results, which will allow participants to review outputs, comment on whether they find them credible and useful, and suggest further refinements.
- **Tech Transfer Webinar.** A planned webinar will support technology transfer of the completed model and products to workshop participants, allowing them to see how their input made it into the final product.
- **Integration into model documentation.** This co-development page, the glossary, and workshop-derived figures will be hosted alongside the developed functions to make the participatory process visible to anyone using or reviewing the simulations.

### 3.4.3 Acknowledgements

The workshop and this co developed model were made possible by the time, knowledge, and care shared by workshop participants and organizers.

#### 3.4.3.1 Participants

Ernie Atkinson  
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# Chapter 4

## Metabolism

### 4.1 Overview

Metabolism determines the energy required for fish to maintain basic physiological function, support movement, regulate ions, digest food, and sustain long term migration. This submodel computes metabolic rate based on size, temperature, age scaling, and allometric relationships. Metabolic efficiency, based on divergence from an agent's optimal temperature, is then scaled toward multiple internal processes including swimming, osmoregulation, and lipid catabolism.

### 4.2 Purpose

To simulate energetically realistic metabolic costs for migratory fishes in coastal and estuarine environments by accounting for size scaling, temperature dependence, age effects, and dynamic energy partitioning across physiological processes.

### 4.3 Entities, State Variables, and Scales

#### 4.3.1 Spatial and Temporal Scales

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

### 4.3.2 Global Variables

Global Variable	Definition
<b>Q10</b>	Temperature coefficient used for metabolic scaling.
<b>base-constant</b>	Global constant for baseline metabolic scaling (0.1).
<b>age-sensitivity</b>	Scalar controlling how metabolism changes with age (0.5).

### 4.3.3 Patch Variables

Variable Name	Definition
<b>temperature</b>	The water temperature of the current patch used to calculate temperature dependent metabolic rate.

### 4.3.4 Agent Variables

Variable Name	Definition
<b>size</b>	Body mass or size index used for allometric scaling.
<b>age-num</b>	Age used in scaling metabolic rate.
<b>optimal-temperature</b>	Preferred temperature at which baseline metabolism is defined.
<b>max-survival-temp</b>	Maximum temperature at which the agent can survive and function.
<b>Met-base</b>	Baseline metabolic constant calculated during initialization.
<b>metabolism-rate</b>	Metabolic rate for the current tick.
<b>total-metabolism</b>	Accumulated metabolism over time.
<b>swim-efficiency</b>	Efficiency applied to movement when metabolic rate is lower or higher than baseline.

Variable Name	Definition
<b>osmoregulation-efficiency</b>	Efficiency applied to osmoregulation when metabolic rate is lower or higher than baseline.
<b>lipid-catabolism-efficiency</b>	Efficiency applied to lipid catabolism when metabolic rate is lower or higher than baseline.
<b>swim-base</b>	Baseline allocation of metabolism toward movement.
<b>E-base</b>	Base metabolic maintenance cost.
<b>E-creation</b>	Energy cost for creating new chloride cells.
<b>E-osmo</b>	Total energy spent on osmoregulation.
<b>motion-ratio</b>	Fraction of metabolism allocated to swimming.
<b>osmo-ratio</b>	Fraction of metabolism allocated to osmoregulation.
<b>M-max</b>	Maximum size for scaling across the population.
<b>max-age</b>	Maximum age for scaling across the population.

## 4.4 Process Overview and Scheduling

1. Retrieve patch temperature and verify safe environmental inputs.
2. Compute allometric, temperature, and age scalars.
3. Calculate metabolic rate for the current tick.
4. Update metabolic accumulation.
5. Compute a reference baseline metabolic rate.
6. Apply efficiency multipliers to swimming, digestion, osmoregulation, and lipid catabolism.

## 4.5 Design Concepts

### Basic Principles:

Metabolic rate combines allometric scaling, temperature responses, and age scaling consistent with metabolic ecology theory. The model uses a Q10 temperature function, Kleiber type allometry, and age dependent reduction in metabolic intensity.

**Emergence:**

Energetic constraints emerge from interactions among size, temperature, and age. These constraints then shape movement, digestion, and osmoregulation.

**Adaptation:**

Agents adapt by adjusting internal efficiencies that influence downstream behavioral and physiological submodels.

**Objectives:**

Agents maintain adequate energy for survival and migration and balance energetic cost across processes.

**Sensing:**

Agents sense the temperature of the patch they occupy.

**Stochasticity:**

The function itself is deterministic but stochastic variation in individual size and age creates emergent metabolic variation.

**Collectives:**

Scaling uses the maximum size and age of the entire population to normalize differences among individuals.

**Observation:**

Outputs include metabolism-rate, total-metabolism, and efficiency multipliers.

## 4.6 Initialization

Variable	Initialized Value	Justification
Met-base	Computed using size, age, and temperature factors	Establishes a physiologically realistic baseline.
swim-base	Met-base times movement ratio	Allocates baseline metabolism for locomotion.
E-base	Met-base times 0.02	Maintenance cost of cellular metabolic activity.
E-creation	Met-base times 0.05	Cost of forming new chloride cells.
motion-ratio	0.7 normalized	Movement is energetically dominant.
osmo-ratio	0.3 normalized	Osmoregulation is energetically significant.
E-osmo	0	No osmoregulation cost at initialization.

Variable	Initialized Value	Justification
metabolism-rate	Met-base	Baseline metabolism in the absence of environmental variation.
total-metabolism	0	Starts accumulation at zero.

## 4.7 Submodels

### 4.7.1 Initialize Metabolism

Baseline metabolic constant is computed using:

$\$ \$ \text{Met-base} = \text{base-constant} (\text{size} / M\text{-max}) ^ {0.75} [1 + \text{age-sensitivity} * (1 - \text{age} / \text{max-age})] * (\text{optimal-temperature} / \text{max-survival-temp}) \$ \$$

Where:

- base-constant is 0.1
- age-sensitivity is 0.5

### 4.7.2 Energy Partitions

Baseline energy partitions are computed from the initialized metabolic base:

$$\text{swim-base} = \text{Met-base} \cdot \text{motion-ratio}$$

$$E_{\text{base}} = \text{Met-base} \cdot 0.02$$

$$E_{\text{creation}} = \text{Met-base} \cdot 0.05$$

### 4.7.3 Metabolic Rate Calculation

At each tick, metabolism is recalculated using allometric, temperature, and age scaling:

$$\text{size-factor} = \left( \frac{\text{weight}}{M\text{-max}} \right)^{0.75}$$

$$\text{temp-factor} = Q_{10}^{\left(\frac{T_{\text{env}} - T_{\text{opt}}}{10}\right)}$$

$$\text{age-factor} = 1 + \left(1 - \frac{\text{age}}{\text{max-age}}\right) \cdot 0.5$$

Total metabolic rate:

$$M_{\text{total}} = \text{Met-base} \cdot \text{size-factor} \cdot \text{temp-factor} \cdot \text{age-factor}$$

Metabolic accumulation:

$$\text{total-metabolism} = \text{total-metabolism} + M_{\text{total}}$$

#### 4.7.4 Efficiency Multipliers

A baseline metabolic reference is defined using:

- baseline size-factor = 1
- baseline age-factor = 1.5
- baseline temp-factor = 1

Thus:

$$M_{\text{baseline}} = \text{Met-base} \cdot 1 \cdot 1 \cdot 1.5$$

Efficiency is computed as:

$$\text{efficiency} = \frac{M_{\text{total}}}{M_{\text{baseline}}}$$

This value is applied to:

- **swim-efficiency**
- **osmoregulation-efficiency**
- **lipid-catabolism-efficiency**

Efficiency dynamically scales the cost of movement, ion regulation, and lipid catabolism.

## 4.8 Netlogo Implementation

```
;; =====
;; METABOLISM SUBMODEL
;; =====

globals [
    ;; global physiological constants
    Q10
]

patches-own [
    temperature
]

fish-own [
    ;; core state variables
    weight
    age-num
    optimal-temperature
    max-survival-temp

    ;; metabolic scalars
    Met-base
    metabolism-rate
    total-metabolism

    ;; efficiency multipliers
    swim-efficiency
    osmoregulation-efficiency
    lipid-catabolism-efficiency

    ;; energy partitioning
    swim-base
    E-base
    E-creation
    E-osmo
    motion-ratio
    osmo-ratio

    ;; population normalization
    M-max
    max-age
]
```

```

;; =====
;;      INITIALIZE METABOLISM
;; =====

to initialize-metabolism
  let beta 0.75
  let age-sensitivity 0.5
  let base-constant 0.1

  ;; normalize population scaling
  set M-max max [weight] of fish
  set max-age max [age-num] of fish
  if M-max <= 0 [ set M-max 1 ]
  if max-age <= 0 [ set max-age 1 ]

  ;; scaling factors
  let size-factor (weight / M-max) ^ beta
  let age-factor 1 + age-sensitivity * (1 - (age-num / max-age))
  let temp-factor (optimal-temperature / max-survival-temp)

  ;; baseline metabolic constant
  set Met-base base-constant * size-factor * age-factor * temp-factor

  ;; energy partitions
  let motion-ratio-local 0.7
  let osmo-ratio-local 0.3
  let total-ratio (motion-ratio-local + osmo-ratio-local)

  set motion-ratio (motion-ratio-local / total-ratio)
  set osmo-ratio (osmo-ratio-local / total-ratio)

  set swim-base (Met-base * motion-ratio)
  set E-osmo 0

  ;; fixed fractions
  set E-base (Met-base * 0.02)
  set E-creation (Met-base * 0.05)

  ;; initial metabolic state
  set metabolism-rate Met-base
  set total-metabolism 0
end

;; =====

```

```

;;      CALCULATE METABOLISM EACH TICK
;; =====

to calculate-metabolism
  let beta 0.75

  ;; repopulate scaling values
  set M-max max [weight] of fish
  set max-age max [age-num] of fish
  if M-max <= 0 [ set M-max 1 ]
  if max-age <= 0 [ set max-age 1 ]

  ;; get patch temperature safely
  let T-env [temperature] of patch-here
  if not is-number? T-env [ set T-env optimal-temperature ]

  ;; scaling factors
  let size-factor (weight / M-max) ^ beta
  let temp-factor Q10 ^ ((T-env - optimal-temperature) / 10)
  let age-factor 1 + (1 - (age-num / max-age)) * 0.5

  ;; metabolic rate (per tick)
  let M-total Met-base * size-factor * temp-factor * age-factor
  set metabolism-rate M-total
  set total-metabolism total-metabolism + M-total

  ;; baseline reference metabolism
  let baseline-size-factor 1
  let baseline-age-factor 1.5
  let baseline-temp-factor 1

  let baseline-metabolism Met-base *
    baseline-size-factor *
    baseline-temp-factor *
    baseline-age-factor

  ;; efficiency multipliers
  let efficiency M-total / baseline-metabolism

  set swim-efficiency          efficiency
  set osmoregulation-efficiency efficiency
  set lipid-catabolism-efficiency efficiency
end

```



# Chapter 5

## Digestion

### 5.1 Overview

Digestion converts consumed prey mass into usable energy and transfers associated contaminants such as inorganic mercury and methylmercury from stomach contents into internal body burden pools. This submodel simulates the breakdown of ingested prey at a rate proportional to the agent's current metabolic rate. As stomach contents are digested, a fraction is converted into energy while mercury and methylmercury are incorporated into the agent's contaminant loads. When stomach contents reach zero, agents transition into foraging mode and begin drawing on lipid reserves.

### 5.2 Purpose

To simulate how migratory fish process ingested prey into energy and contaminants while linking digestive performance to metabolic rate, foraging behavior, and exposure risk. Digestion provides the energetic foundation required for movement, migration, and physiological processes while directly influencing contaminant accumulation.

### 5.3 Entities, State Variables, and Scales

#### 5.3.1 Spatial and Temporal Scales

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

### 5.3.2 Global Variables

Global Variable	Definition
<b>none required</b>	Digestion uses internal agent state + metabolism-rate from metabolism submodel.

### 5.3.3 Patch Variables

Variable Name	Definition
None required	Digestion is an internal physiological process and does not depend on patch attributes.

### 5.3.4 Agent Variables

Variable Name	Definition
<b>stomach-contents</b>	Total mass of prey currently held in the stomach.
<b>stomach-contents-Hg</b>	Inorganic mercury contained within the stomach contents.
<b>stomach-contents-MeHg</b>	Methylmercury contained within the stomach contents.
<b>digestion-rate</b>	Rate of digestion equal to the current metabolic rate.
<b>digestion-efficiency</b>	Fraction of digested mass converted into usable energy.
<b>energy</b>	Total energetic reserves available to the agent.
<b>gained-energy</b>	Energy gained during the current tick from digestion.
<b>mehg-foraging</b>	Methylmercury released from stomach contents and absorbed during digestion.
<b>hg-foraging</b>	Inorganic mercury released from stomach contents during digestion.
<b>mehg-foraging-total</b>	Cumulative methylmercury risk through feeding.

Variable Name	Definition
<b>hg-foraging-total</b>	Cumulative inorganic mercury risk via digestion.
<b>mehg-total</b>	Total body burden of methylmercury risk.
<b>hg-total</b>	Total body burden of inorganic mercury risk.
<b>foraging</b>	Boolean indicating whether the agent is actively searching for prey.
<b>lipid-loss</b>	Boolean indicating when lipid reserves are used due to lack of stomach content.

## 5.4 Process Overview and Scheduling

1. Set digestion rate equal to the current metabolic rate.
2. Calculate the mass digested during the current tick.
3. Compute the corresponding amounts of inorganic and methylmercury digested.
4. Remove digested prey mass and associated contaminants from stomach contents.
5. Convert a fraction of digested biomass into usable energy.
6. Add mercury and methylmercury to cumulative body burden pools.
7. When stomach contents reach zero, set foraging to true and begin lipid use.

## 5.5 Design Concepts

### Basic Principles:

Digestion is modeled as a metabolic rate dependent process, where higher metabolic demand results in greater digestive throughput. Contaminants are transferred into the agent's body burden proportionally to the fraction of mass digested.

**Emergence:**

Patterns of energy gain and contaminant uptake emerge from interactions among foraging success, metabolism, digestion efficiency, and prey availability.

**Adaptation:**

Agents respond to depleted stomach contents by transitioning into foraging mode and initiating lipid catabolism when necessary.

**Objectives:**

Agents maximize energetic intake to support migration, physiological function, and survival while minimizing energetic deficits.

**Sensing:**

Agents sense their own energetic state through stomach contents and energy levels.

**Stochasticity:**

Stochasticity arises indirectly from variation in prey encounters or foraging success, although digestion itself is deterministic.

**Collectives:**

Digestion occurs independently for each agent and does not require group level dynamics.

**Observation:**

Outputs of interest include digested mass per tick, gained energy, contaminant uptake, and cumulative contaminant burdens.

## 5.6 Initialization

Variable	Initialized Value	Justification
stomach-contents	0	Agents begin without prey unless defined by scenario.
stomach-contents-Hg	0	No initial inorganic mercury from digestion.
stomach-contents-MeHg	0	No initial methylmercury from digestion.
digestion-efficiency	Species specific	Determines fraction of biomass converted to energy.
foraging	true	Agents begin in search mode when stomach is empty.

## 5.7 Submodels

### 5.7.1 Digestion Rate and Breakdown

Digestive throughput is driven by metabolic rate:

$$\text{digestion-rate} = \text{metabolism-rate}$$

Digested mass per tick:

$$\text{digested} = \text{stomach-contents} \cdot \text{digestion-rate}$$

Proportional mercury assimilation:

$$\text{digested-Hg} = \left( \frac{\text{digested}}{\text{stomach-contents}} \right) \cdot \text{stomach-contents-Hg}$$

$$\text{digested-MeHg} = \left( \frac{\text{digested}}{\text{stomach-contents}} \right) \cdot \text{stomach-contents-MeHg}$$

Updated stomach contents:

$$\text{stomach-contents} = \text{stomach-contents} - \text{digested}$$

### 5.7.2 Energy Conversion

Energy gained from digestion:

$$\text{gained-energy} = \text{digested} \cdot \text{digestion-efficiency} \cdot 40$$

Updated energy pool:

$$\text{energy} = \text{energy} + \text{gained-energy}$$

### 5.7.3 Contaminant Assimilation

Contaminants absorbed during digestion:

$$\text{mehg-foraging} = \text{digested-MeHg}$$

$$hg\text{-}foraging = digested\text{-}Hg$$

Accumulated body burden:

$$mehg\text{-}total = mehg\text{-}total + digested\text{-}MeHg$$

$$hg\text{-}total = hg\text{-}total + digested\text{-}Hg$$

#### 5.7.4 Transition to Foraging

When stomach contents reach zero:

- lipid-loss is activated

This switches the prey to burn fat energy reserves instead of relying on stomach contents.

### 5.8 Netlogo Implementation

```
;; =====
;; DIGESTION SUBMODEL
;; =====

fish-own [
    ; digestion state
    stomach-contents
    stomach-contents-Hg
    stomach-contents-MeHg
    digestion-rate
    digestion-efficiency

    ; contaminant tracking
    mehg-foraging
    hg-foraging
    mehg-foraging-total
    hg-foraging-total
    mehg-total
    hg-total
```

```

;; energy + biomass
energy
weight
lipid-loss
lipid-catabolism-efficiency
]

to digest
  ;; digestion tied to metabolic rate
  set digestion-rate metabolism-rate

  ;; nothing to digest
  if stomach-contents <= 0 [
    set foraging true
    set lipid-loss true
    stop
  ]

  ;;;;;;;;;;;;;;;;;;;;;;;;;;
  ;;; DIGESTIVE BREAKDOWN
  ;;;;;;;;;;;;;;;;;;;;;;;;;;

  ;; amount of prey broken down this tick
  let digested (stomach-contents * digestion-rate)

  ;; numerical guard to avoid divide-by-zero
  if stomach-contents <= 0.000001 [ set digested 0 ]

  let digested-Hg 0
  let digested-MeHg 0

  if digested > 0 and stomach-contents > 0 [
    set digested-Hg ((digested / stomach-contents) * stomach-contents-Hg)
    set digested-MeHg ((digested / stomach-contents) * stomach-contents-MeHg)
  ]

  ;;;;;;;;;;;;;;;;;;;;;;;;;;
  ;;; UPDATE STOMACH CONTENTS
  ;;;;;;;;;;;;;;;;;;;;;;;;;;

  set stomach-contents (max list 0 (stomach-contents - digested))
  set stomach-contents-Hg (max list 0 (stomach-contents-Hg - digested-Hg))
  set stomach-contents-MeHg (max list 0 (stomach-contents-MeHg - digested-MeHg))

  ;;;;;;;;;;;;;;;;;;;;;;;;;;

```

```

;; ENERGY CONVERSION
;; =====

let usable-energy (digested * digestion-efficiency * 40)
set energy energy + usable-energy

;; =====
;; STORE LIPID IF ENERGY SURPLUS
;; =====

if energy > 100 [
  let surplus (energy - 100)

  ;; convert surplus to lipid
  let lipid-added (surplus / 40)

  ;; apply storage efficiency
  set lipid-added (lipid-added * lipid-catabolism-efficiency)

  ;; update biomass
  set weight weight + lipid-added

  ;; subtract energy equivalent
  set energy energy - (lipid-added * 40)
]

;; =====
;; CONTAMINANT ASSIMILATION
;; =====

set mehg-foraging      digested-MeHg
set hg-foraging        digested-Hg
set mehg-foraging-total mehg-foraging-total + digested-MeHg
set hg-foraging-total  hg-foraging-total + digested-Hg
set mehg-total          mehg-total + digested-MeHg
set hg-total            hg-total + digested-Hg

;; =====
;; SWITCH TO Lipid Loss IF EMPTY
;; =====

if stomach-contents <= 0 [
  set lipid-loss true
]
end

```

# Chapter 6

## Salinity Exposure

### 6.1 Overview

Osmoregulation allows migratory fish to maintain homeostasis by regulating internal ion concentrations in response to varying environmental salinities. This function simulates salinity exposure through ion-regulatory stress, chloride cell expression, and the metabolic energy cost of acclimating to this exposure internally in a spatiotemporal explicit context.

### 6.2 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.

### 6.3 Entities, State Variables, and Scales

#### 6.3.1 Spatial and Temporal Scales

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

#### 6.3.2 Global Variables

	Global Variable	Definition
<b>none required</b>		Salinity exposure uses internal agent state

### 6.3.3 Patch Variables

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

### 6.3.4 Agent Variables

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

Variable Name	Definition
<b>metabolic-max</b> $Met_{max}$	Maximum metabolic cost for chloride cell creation.

## 6.4 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.

## 6.5 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  $\alpha$ , 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.

## 6.6 Initialization

Variable	Value	Initialized 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.
$C_{max}$	100%	Agents can't express more than 100% of cells.
$\alpha$	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%) Apterygian ()	Based on the <b>branchial cost</b> (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.

## 6.7 Submodels

### 6.7.1 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.

### 6.7.2 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),  $\backslash(C_{\{target\}}\backslash)$  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:

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

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

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.
- $\Delta C$  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.
- $\alpha$  is the acclimation rate constant.
- $t_{osmo}$  represents time since the last osmoregulation event.

## Osmoregulation Energy

Metabolic cost related to size:

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

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.

### 6.7.3 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.

```
;; =====
;; SALINITY EXPOSURE AND OSMOREGULATION SUBMODEL
;; =====

globals [
  stable-time           ;; tracks duration of stable salinity
  salinity-threshold    ;; threshold difference to count as "stable"
]

patches-own [
  salinity              ;; environmental salinity (psu)
```

```

]

fish-own [
    ;; --- Salinity Physiology ---
    acclimated-salinity
    ionregulatory-stress      ;; 1-10 scale

    ;; --- Chloride Cell Physiology ---
    chloride-density-min
    chloride-density-max
    chloride-cell-density
    chloride-max-proliferation
    chloride-cells-this-tick
    C-mid

    ;; --- Acclimation Timing ---
    acclimation-rate
    time-since-last-osmoregulation

    ;; --- Energetics ---
    energy
    E-osmo
    E-base
    E-creation
    Met-max

    ;; --- Size Scaling ---
    weight
]

;; =====
;; MAIN OSMOREGULATION PROCEDURE
;; =====

to osmoregulate
    calculate-ionregulatory-stress
    regulate-chloride-cell-density
    calculate-osmoregulation-energy
end

;; =====
;; STEP 1 - CALCULATE ION-REGULATORY STRESS
;; =====

```

```

to calculate-ionregulatory-stress
  let prev-sal [salinity] of previous-patch
  let patch-sal [salinity] of patch-here
  let agent-sal acclimated-salinity

  ;; --- Base salinity difference ---
  let sal-diff abs (agent-sal - patch-sal)

  ;; --- Core salinity-based stress function ---
  let salinity-stress salinity-to-stress sal-diff chloride-cell-density ionregulatory-stress

  ;; --- Salinity stability, used for acclimation ---
  let sal-change abs (patch-sal - prev-sal)

  if sal-change < salinity-threshold [
    set stable-time stable-time + 1
  ]
  if sal-change >= salinity-threshold [
    set stable-time 0
  ]

  ;; --- Slow acclimation when salinity is stable ---
  if stable-time > 4 and chloride-cell-density > chloride-density-min [
    set salinity-stress salinity-stress * 0.98
    set acclimated-salinity acclimated-salinity +
      ((patch-sal - acclimated-salinity) * 0.02)
  ]

  ;; --- Chloride buffering ---
  let buffer-reduct calculate-stress-reduction-chloride-function chloride-cell-density

  ;; Buffering only applies above minimum chloride levels
  if chloride-cell-density > chloride-density-min [
    set ionregulatory-stress max (list 1 (salinity-stress - buffer-reduct * 0.8))
  ]

  if chloride-cell-density <= chloride-density-min [
    set ionregulatory-stress salinity-stress
  ]
end

;; =====
;; STEP 2 - REGULATE CHLORIDE CELL DENSITY
;; =====

```

```

to regulate-chloride-cell-density
  ;;= energetic constraint
  if energy <= 25 [ stop ]

  set time-since-last-osmoregulation time-since-last-osmoregulation + 1

  ;;= wait until acclimation interval
  if time-since-last-osmoregulation < acclimation-rate [ stop ]

  ;;= --- Target chloride cell density ---
  let target-dens chloride-density-min +
    ((chloride-density-max - chloride-density-min) *
     (ionregulatory-stress / 10))

  ;;= down-regulate if long-term stability
  if stable-time > 288 [
    set target-dens (target-dens * 0.99)
  ]

  ;;= constrain target to bounds
  set target-dens max (list chloride-density-min
                        min (list chloride-density-max target-dens))

  ;;= --- Adjustment rate ---
  let change (target-dens - chloride-cell-density) *
    (2 * chloride-max-proliferation)

  let max-change ((chloride-density-max - chloride-density-min) *
                  chloride-max-proliferation)

  ;;= clamp change
  set change max (list (-1 * max-change) (min (list max-change change)))

  ;;= energy-dependent reduction
  if energy <= 50 [
    set change (change * 0.5)
  ]

  ;;= apply change
  set chloride-cell-density chloride-cell-density + change
  set chloride-cell-density max (list chloride-density-min
                                min (list chloride-density-max chloride-cell-density))

  set chloride-cells-this-tick abs change
  set time-since-last-osmoregulation 0

```

```

end

;; =====
;; STEP 3 - OSMOREGULATION ENERGY COST
;; =====

to calculate-osmoregulation-energy
  let maintenance (E-base * chloride-cell-density)
  let creation      (E-creation * chloride-cells-this-tick)

  set E-osmo (maintenance + creation)
  set energy max (list 0 (energy - E-osmo))
end

;; =====
;; CHLORIDE BUFFERING FUNCTION
;; =====

to-report calculate-stress-reduction-chloride-function [C]
  ; logistic-like buffering curve
  let reduction 5 * (1 - exp(C * -0.5 / C-mid))
  report reduction
end

;; =====
;; SALINITY → STRESS FUNCTION
;; =====

to-report salinity-to-stress [diff C prev-stress]
  let scaled (log (1 + abs diff) 10) * 10
  let buffer  (1 + exp(-2 * (C / C-mid)))
  let result  (scaled / buffer)

  ; constrain to 1-10
  set result max (list 1 (min (list 10 result)))

  ; acclimation effect
  if stable-time > 288 [
    set result (result * 0.99)
  ]

  report result

```

```
end

;; =====
;; SIZE-SCALED CREATION COST
;; =====

to calculate-E-creation
  let M-max max [weight] of fish
  if M-max <= 0 [ set M-max weight ]

  let beta -0.75
  set E-creation Met-max * ((weight / M-max) ^ beta)
end
```

# Chapter 7

## Migration Cues

### 7.1 Overview

This submodel simulates how migratory fish detect environmental cues that signal the onset of migration. The mechanism is grounded in empirical evidence that **simultaneous declines in daylength and temperature** reliably precede the initiation of seaward migration in several anadromous species. In this model, migration begins only when a fish experiences environmental conditions consistent with an autumnal cue window defined by:

- A **decline in daylength**

$$\Delta L < 0$$

- A **decline in temperature**

$$\Delta T < 0$$

- And these declines occurring **on the same day**, indicating a **coincident decline**

When this occurs, the day is labeled a *cue day*. Upon reaching cue days, individuals begin stochastically accumulating the probability of initiating migration. For predators (striped bass), migration probability additionally depends on alewife presence, linking species interactions to migration onset.

## 7.2 Purpose

The purpose of this submodel is to mechanistically trigger migration using **real, observed environmental phenology** rather than arbitrary or date-based rules. This framework captures how:

- Changes in  $\Delta$ Temperature and  $\Delta$ Daylength structure seasonality
- Migration timing emerges pragmatically rather than being fixed
- Fish respond to external conditions and species interactions
- Environmental preprocessing in R feeds into NetLogo behavioral rules

This allows migration in the model to originate from measurable ecological drivers instead of hard-coded thresholds.

## 7.3 Entities, State Variables, and Scales

### 7.3.1 Spatial and Temporal Scales

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

### 7.3.2 Global Variables

Global Variable	Definition
<b>cue-table</b>	Lookup table containing $\Delta$ Temperature, $\Delta$ Daylength, their smoothed values, and Boolean coincident-decline flags (from R preprocessing)
<b>cue-days</b>	List of day-of-year values where $\Delta T < 0$ and $\Delta L < 0$ simultaneously (identified in R)
<b><math>\Delta T</math></b>	Daily rate of change in temperature imported from R ( <b>dT_per_day_f</b> or smoothed <b>dT_smooth</b> )

Global Variable	Definition
<b>ΔL</b>	Daily rate of change in photoperiod imported from R (dL_per_day_min or smoothed dL_smooth)
<b>cue-active?</b>	Whether the current day-of-year corresponds to a coincident decline day
<b>migration-trigger?</b>	Whether environmental signals are strong enough to begin building migration probability

### 7.3.3 Patch Variables

Migration cues do not depend on patch-level conditions. No patch-scale variables are required.

### 7.3.4 Agent Variables

Variable	Definition
<b>migration-trigger?</b>	Whether the agent has entered a window where migration probability begins to accumulate
<b>migration-probability</b>	The cumulative probability of initiating migration, updated each tick once the trigger is active
<b>start-migration?</b>	Whether the individual has begun active migration

## 7.4 Process Overview and Scheduling

### 7.4.1 1. Environmental Inputs (from R)

External R preprocessing computes:

- $\Delta$ Temperature per day
- $\Delta$ Daylength per day

- Smoothed 3-day rolling means
- Boolean `both_negative` indicating coincident decline
- Exports full dataset as "`cue_dataset_full.csv`"

This dataset defines the environmental basis for triggering migration.

#### 7.4.2 2. Identify Cue Days

Cue days are those where:

$$\Delta T < 0 \quad \wedge \quad \Delta L < 0$$

The model loads the CSV at setup and extracts all days meeting this criterion into `cue-days`.

#### 7.4.3 3. Activate Cue

Each simulation day checks whether:

$$\text{day-of-year} \in \text{cue-days}$$

If true, then:

- `cue-active? = true`
- `migration-trigger? = true`

This marks the environmental onset of migration preparedness.

#### 7.4.4 4. Alewife Migration Probability Accumulation

Once the migration trigger is active, each tick adds:

$$\text{migration\_probability}_{t+1} = \text{migration\_probability}_t + (0.00001 + U(0, 0.00004))$$

Capped at:

$$\text{migration\_probability} \leq 1$$

This produces:

- Individual variation in migration timing
- Realistic ramping into migration
- Stochastic onset probabilities

#### 7.4.5 5. Initiation of Migration

An agent begins migration when:

`random-float(1) < migration_probability`

At this moment:

- `start-migration? = true`
- Movement functions shift from staging to directed migration

## 7.5 Design Concepts

### Basic Principles

The mechanism reflects literature on photoperiod- and temperature-driven migration cues.

### Emergence

Migration timing varies among individuals because probability increments differ slightly with stochasticity.

### Observation

Key outputs: cue day activation, probability trajectories, proportion of migrants through time.

## 7.6 Initialization

Variable	Initial Value	Justification
<code>cue-days</code>	Extracted from CSV	Based on empirical environmental data
<code>migration-probability</code>	0	Ensures probability is accumulated only within cue window
<code>migration-trigger?</code>	false	No cue until $\Delta T$ and $\Delta L$ decline

Variable	Initial Value	Justification
<b>cue-active?</b>	false	Depends on DOY
<b>start-migration?</b>	false	Fish begin in staging mode

## 7.7 Submodels

### 7.8 1. Identifying Cue Days (Preprocessed in R)

$$\Delta T < 0, \quad \Delta L < 0$$

The preprocessing script:

1. Computes  $\Delta T$  and  $\Delta L$
2. Applies smoothing
3. Flags coincident declines

### 7.9 2. Alewife Migration Probability

$$migration\_probability_{t+1} = migration\_probability_t + (0.00001 + U(0, 0.00004))$$

$$migration\_probability \leq 1$$

### 7.10 Netlogo Implementation

```
;; -----
;;  GLOBALS
;; -----
globals [
  cue-table
  cue-days

  migration-trigger?
  cue-active?
]

;; -----
```

```

;; TURTLE VARIABLES
;; -----
turtles-own [
  migration-probability
  start-migration?
]

;; -----
;; LOAD CUE DATA (CSV FROM R)
;; -----
to load-cue-csv
  set cue-table table:make
  let raw csv:from-file "inputs/cue_dataset_full.csv"

  let header first raw
  let rows but-first raw

  foreach rows [
    r ->
    let doy      item 7 r
    let dTsm     item 21 r
    let dLsm     item 22 r
    let negflag  item 24 r

    table:put cue-table doy (list dTsm dLsm negflag)
  ]
end

;; -----
;; IDENTIFY CUE DAYS ( $\Delta T < 0$  AND  $\Delta L < 0$ )
;; -----
to find-migration-days
  set cue-days []

  foreach sort table:keys cue-table [
    d ->
    let vals table:get cue-table d
    let negflag item 2 vals

    if (negflag = "TRUE" or negflag = true) [
      set cue-days lput d cue-days
    ]
  ]
end

```

```
;; -----
;;  UPDATE MIGRATION CUE (DAILY)
;; -----
to update-migration-cue
  ifelse member? day cue-days [
    set cue-active? true
    set migration-trigger? true
  ] [
    set cue-active? false
  ]
end

;; -----
;;  ALEWIFE MIGRATION PROBABILITY ACCUMULATION
;; -----
to calc-migration-probability
  if migration-trigger? [
    set migration-probability
      migration-probability
      + (0.00001 + random-float 0.00004)

    if migration-probability > 1 [
      set migration-probability 1
    ]
  ]
end

to migrate
  if random-float 1 <= migration-probability
  set start-migration? true
end
```

# Chapter 8

# Contaminant Exposure

## 8.1 Overview

The contaminant exposure submodel simulates mercury and methylmercury exposure risk across gills for migratory fish moving through spatially and temporally variable contamination fields. Exposure risk depends on contaminant concentration, suspended particulate matter, and metabolic rate. Concentrations of mercury and methylmercury are normalized across the spatial domain, and depth averaged SPM values modulate risk to reflect particle bound contaminant transport. Agents accumulate both instantaneous and cumulative exposure, allowing estimation of bioaccumulation risk over the migration season.

## 8.2 Purpose

To evaluate mercury and methylmercury exposure and bioaccumulation risk for migratory fishes by integrating patch level contamination, ionregulatory stress, depth averaged suspended particulate matter, and metabolism driven uptake processes in estuarine and coastal systems.

## 8.3 Entities, State Variables, and Scales

### 8.3.1 Spatial and Temporal Scales

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

### 8.3.2 Global Variables

Variable	Initialized Value	Justification
<b>MeHg-threshold</b>	15 ug per kg	Screening threshold for methylmercury (??)
<b>Hg-threshold</b>	150 ug per kg	NOAA guideline for mercury contamination (??)
<b>min-Hg, max-Hg</b>	Calculated from input layers	Required for Hg normalization across domain
<b>min-MeHg, max-MeHg</b>	Calculated from input layers	Required for MeHg normalization across domain

### 8.3.3 Patch Variables

Variable Name	Definition
<b>mercury</b>	Mercury concentration at this patch.
<b>methylmercury</b>	Methylmercury concentration at this patch.
<b>SPM</b>	Depth averaged suspended particulate matter at this patch.
<b>Hg-exp-risk-alewife</b>	Patch level mercury exposure risk from alewives.
<b>Hg-exp-risk-stripedbass</b>	Patch level mercury exposure risk from striped bass.
<b>MeHg-exp-risk-alewife</b>	Patch level methylmercury risk from alewives.
<b>MeHg-exp-risk-stripedbass</b>	Patch level methylmercury risk from striped bass.

### 8.3.4 Agent Variables

Variable Name	Definition
<b>metabolism-rate</b>	Current metabolic rate used to scale uptake risk.
<b>hg-exposure-duration</b>	Number of ticks spent above the mercury threshold.

Variable Name	Definition
<b>mehg-exposure-duration</b>	Number of ticks spent above the MeHg threshold.
<b>hg-uptake-risk</b>	Instantaneous mercury uptake risk per tick.
<b>mehg-uptake-risk</b>	Instantaneous methylmercury uptake risk per tick.
<b>hg-total</b>	Cumulative mercury uptake.
<b>mehg-total</b>	Cumulative methylmercury uptake.
<b>hg-exposure-total</b>	Total non normalized Hg exposure.
<b>mehg-exposure-total</b>	Total non normalized MeHg exposure.
<b>hg-exposure-total-normalized</b>	Sum of normalized Hg exposure values.
<b>mehg-exposure-total-normalized</b>	Sum of normalized MeHg exposure values.

## 8.4 Process Overview and Scheduling

1. Retrieve mercury, methylmercury, and depth averaged SPM values from the current patch.
2. Normalize patch contaminants between 0 and 1.
3. Compare patch levels to stress thresholds.
4. Update exposure durations.
5. Compute uptake risk using metabolism, ionregulatory stress, and SPM.
6. Add uptake risk to cumulative body burden.
7. Update patch level species specific risk metrics.

## 8.5 Design Concepts

### Basic Principles:

Contaminant uptake follows toxicokinetic principles where absorption increases with concentration, metabolic rate, and suspended particulate matter (SPM).

Depth averaged SPM reflects hydrodynamic transport and particle bound contaminant processes for fish typically found near the middle of the water column.

**Emergence:**

Exposure and risk patterns emerge from individual movement across heterogeneous contamination fields coupled with metabolic and stress driven physiology.

**Adaptation:**

Agents do not actively avoid contamination, but their internal physiology modulates uptake in response to metabolic changes.

**Objectives:**

This model does not give agents risk minimization behavior. Instead, risk is assessed to evaluate means of exposure pathways and cumulative toxic exposure.

**Sensing:**

Agents sense patch level mercury, methylmercury, SPM, and internal metabolic state.

**Stochasticity:**

Variation in spatial contaminant fields or individual characteristics and state creates stochastic variation in exposure.

**Observation:**

Outputs include instantaneous exposure risk, cumulative exposure risk, normalized exposure totals, and patch level species specific contributions.

## 8.6 Initialization

Variable	Initialized Value	Justification
mercury	Input layer	Hydrodynamic or field derived contaminant layer.
methylmercury	Input layer	Same as above.
SPM	Depth averaged input	Reflects hydrodynamic particle transport.

## 8.7 Submodels: Mercury Exposure and Uptake

### 8.7.1 Normalization

$$Hg_{normalized} = \frac{Hg_{current} - minHg}{maxHg - minHg}$$

Bounded in the range 0 to 1.

### 8.7.2 Exposure Duration

$$Hg_{exp} = Hg_{exp} + 1 \quad \text{if } Hg_{current} > Hg_{threshold}$$

### 8.7.3 Uptake Risk

$$Hg_{risk} = metabolism \cdot Hg_{normalized} \cdot (1 + S) \cdot (1 + SPM)$$

### 8.7.4 Cumulative Uptake

$$Hg_{total} = Hg_{total} + Hg_{risk}$$

Patch level storage based on species for cumulative duration risk experience in space:

- Hg-exp-risk
- Hg-exp-risk

## 8.8 Submodels: Methylmercury Exposure and Uptake

### 8.8.1 Normalization

$$MeHg_{normalized} = \frac{MeHg_{current} - minMeHg}{maxMeHg - minMeHg}$$

Clamped to the range 0 to 1.

### 8.8.2 Exposure Duration

$$MeHg_{exp} = MeHg_{exp} + 1 \quad \text{if } MeHg_{current} > MeHg_{threshold}$$

### 8.8.3 Uptake Risk

$$MeHg_{risk} = metabolism \cdot MeHg_{normalized} \cdot (1 + S) \cdot (1 + SPM)$$

### 8.8.4 Cumulative Uptake

$$MeHg_{total} = MeHg_{total} + MeHg_{risk}$$

Patch level storage based on species for cumulative duration risk experience in space:

- MeHg-exp-risk
- MeHg-exp-risk

```
globals [
    ;; Thresholds
    MeHg-threshold
    Hg-threshold

    ;; Domain-wide normalization bounds
    min-Hg
    max-Hg
    min-MeHg
    max-MeHg
]

patches-own [
    ;; Contaminant inputs
    mercury
    methylmercury
    SPM

    ;; Species-specific instantaneous risk
    Hg-exp-risk-alewife
    Hg-exp-risk-stripedbass
    MeHg-exp-risk-alewife
    MeHg-exp-risk-stripedbass

    ;; Species-specific cumulative patch totals
    Hg-exp-risk-total-alewife
    Hg-exp-risk-total-stripedbass
    MeHg-exp-risk-total-alewife
    MeHg-exp-risk-total-stripedbass
]

turtles-own [
    ;; Physiology
    metabolism-rate
```

```

ionregulatory-stress

;; Exposure durations
hg-exposure-duration
mehg-exposure-duration

;; Instantaneous uptake
hg-uptake-risk
mehg-uptake-risk

;; Cumulative uptake
hg-total
mehg-total

;; Cumulative exposure raw
hg-exposure-total
mehg-exposure-total

;; Cumulative normalized exposure
hg-exposure-total-normalized
mehg-exposure-total-normalized
]

;; =====
;; MERCURY EXPOSURE
;; =====

to mercury-contamination

;; -----
;; Retrieve patch contaminant and SPM values
;; -----
let Hg-current [mercury] of patch-here
let SPM-current [SPM] of patch-here

if not is-number? Hg-current [ set Hg-current 0 ]
if not is-number? SPM-current [ set SPM-current 0 ]

;; -----
;; Normalize Hg concentration (0-1)
;; -----
let Hg-normalized 0
if (max-Hg - min-Hg) > 0 [
  set Hg-normalized (Hg-current - min-Hg) / (max-Hg - min-Hg)
]

```

```

;; clamp
set Hg-normalized max list 0 (min list 1 Hg-normalized)

;; -----
;; Exposure duration: threshold exceedance
;;
if Hg-current > Hg-threshold [
    set hg-exposure-duration hg-exposure-duration + 1
]

;; -----
;; Uptake risk (toxicokinetic rule)
;;
let stress-factor (1 + ionregulatory-stress)
let spm-factor      (1 + SPM-current)

set hg-uptake-risk (metabolism-rate * Hg-normalized * stress-factor * spm-factor)

;; no negative risk ever
if hg-uptake-risk < 0 [ set hg-uptake-risk 0 ]

;; -----
;; Add to cumulative body burden
;;
set hg-total hg-total + hg-uptake-risk

;; -----
;; Track cumulative raw & normalized exposure
;;
set hg-exposure-total          hg-exposure-total + Hg-current
set hg-exposure-total-normalized hg-exposure-total-normalized + Hg-normalized

;; -----
;; Patch-level risk recording (species specific)
;;
let patch-risk hg-uptake-risk

if breed = alewives [
    ask patch-here [
        set Hg-exp-risk-alewife      patch-risk
        set Hg-exp-risk-total-alewife (Hg-exp-risk-total-alewife + patch-risk)
    ]
]

if breed = stripedbass [

```

```

ask patch-here [
  set Hg-exp-risk-stripedbass      patch-risk
  set Hg-exp-risk-total-stripedbass (Hg-exp-risk-total-stripedbass + patch-risk)
]
]

end

;; =====
;; METHYLMERCURY EXPOSURE
;; =====

to methylmercury-contamination

;; -----
;; Retrieve patch contaminant and SPM values
;;
let MeHg-current [methylmercury] of patch-here
let SPM-current [SPM] of patch-here

if not is-number? MeHg-current [ set MeHg-current 0 ]
if not is-number? SPM-current [ set SPM-current 0 ]

;; -----
;; Normalize MeHg concentration (0-1)
;;
let MeHg-normalized 0
if (max-MeHg - min-MeHg) > 0 [
  set MeHg-normalized (MeHg-current - min-MeHg) / (max-MeHg - min-MeHg)
]

;; clamp
set MeHg-normalized max list 0 (min list 1 MeHg-normalized)

;; -----
;; Exposure duration: threshold exceedance
;;
if MeHg-current > MeHg-threshold [
  set mehg-exposure-duration mehg-exposure-duration + 1
]

;; -----
;; Uptake risk
;;

```

```

let stress-factor (1 + ionregulatory-stress)
let spm-factor      (1 + SPM-current)

set mehg-uptake-risk (metabolism-rate * MeHg-normalized * stress-factor * spm-factor)

if mehg-uptake-risk < 0 [ set mehg-uptake-risk 0 ]

;; -----
;; Add to cumulative body burden
;; -----
set mehg-total mehg-total + mehg-uptake-risk

;; -----
;; Track cumulative raw & normalized exposure
;; -----
set mehg-exposure-total           mehg-exposure-total + MeHg-current
set mehg-exposure-total-normalized mehg-exposure-total-normalized + MeHg-normalized

;; -----
;; Patch-level risk recording (species specific)
;; -----
let patch-risk mehg-uptake-risk

if breed = alewives [
  ask patch-here [
    set MeHg-exp-risk-alewife      patch-risk
    set MeHg-exp-risk-total-alewife (MeHg-exp-risk-total-alewife + patch-risk)
  ]
]

if breed = stripedbass [
  ask patch-here [
    set MeHg-exp-risk-stripedbass   patch-risk
    set MeHg-exp-risk-total-stripedbass (MeHg-exp-risk-total-stripedbass + patch-risk)
  ]
]

end

```

# Chapter 9

## Filter Feeding

### 9.1 Overview

Filter feeding is a foraging behavior in which fish consume suspended particulate matter as they migrate through estuarine and coastal systems. In this submodel, agents evaluate neighboring patches based on suspended particulate matter concentration and selectively filter feed where energetic return is highest. Filtration capacity increases with body size, metabolic rate, and digestion efficiency, and is reduced under competition from other filter feeding fish. Contaminant loads in the water column directly influence mercury and methylmercury assimilation during feeding, including biomagnification effects.

### 9.2 Purpose and Patterns

The purpose of this submodel is to simulate ecologically realistic filter feeding behavior in migratory fish using suspended particulate matter as a food resource. This behavior links hydrodynamic particle fields to energy gain, contaminant exposure, and movement decisions. Filter feeding only occurs when spatial conditions and energetic returns are favorable, and incorporates competition, biomagnification, and digestion constraints.

This submodel represents the following ecological patterns:

- **Filtration capacity increases with body size, metabolism, and digestive efficiency**

Larger individuals with higher metabolism filter more water and assimilate more prey mass.

- **Gaussian SPM preference centered on optimal SPM**  
Feeding intensity is highest near an optimal SPM range and decreases away from that peak.
- **Crowding penalty from con-specifics**  
Filtration benefit decreases when multiple individuals feed in the same patch.
- **Movement toward highest benefit**  
Fish move toward the patch with the highest filtration benefit based on SPM and competitive pressure.
- **Contaminant assimilation tied directly to filtration**  
Mercury and methylmercury are assimilated proportionally to SPM concentration and biomagnification factors derived from empirical trophic magnification relationships.

## 9.3 Entities, State Variables, and Scales

### 9.3.1 Spatial and Temporal Scales

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

### 9.3.2 Global Variables

Global Variable	Definition
<b>spm-sd</b>	Standard deviation for Gaussian SPM preference curve (controls width of feeding preference)
<b>max-filter-distance</b>	Maximum distance within which patches can be evaluated (optional, model dependent)
<b>BMF-MeHg</b>	Biomagnification factor for methylmercury ( 1.74; after Lavoie et al. 2013)
<b>BMF-Hg</b>	Biomagnification factor for inorganic Hg ( 1.38; after Lavoie et al. 2013)
<b>previous-x</b>	X-coordinate of agent's previous location (used to compute travel distance and energy cost)
<b>previous-y</b>	Y-coordinate of agent's previous location (used with previous-x)

### 9.3.3 Patch Variables

Variable Name	Definition
<b>SPM</b>	Suspended particulate matter concentration in the water column
<b>mercury</b>	Inorganic mercury concentration at the patch
<b>methylmercury</b>	Methylmercury concentration at the patch
<b>patch-terrain</b>	Identifies water or land patches

### 9.3.4 Agent Variables

Variable Name	Definition
<b>size</b>	Body size used to scale filtration capacity
<b>weight</b>	Biomass used in base filtration scaling (from metabolism submodel)
<b>metabolism-rate</b>	Metabolic rate that modulates filtration intensity
<b>digestion-efficiency</b>	Fraction of filtered biomass digested
<b>optimal-SPM</b>	SPM concentration where filtration is most efficient
<b>filter-feed?</b>	Boolean indicating whether the agent engages in filter feeding
<b>energy</b>	Current energy reserves
<b>E-swim</b>	Energy cost of swimming per meter
<b>swim-efficiency</b>	Efficiency of movement based on metabolic state
<b>speed</b>	Swimming speed
<b>stomach-contents</b>	Biomass currently held in the stomach
<b>stomach-capacity</b>	Maximum biomass that can be held
<b>stomach-contents-Hg</b>	Inorganic mercury within stomach contents
<b>stomach-contents-MeHg</b>	Methylmercury within stomach contents
<b>hg-total</b>	Total cumulative inorganic mercury body burden
<b>mehg-total</b>	Total cumulative methylmercury body burden

Variable Name	Definition
<b>hg-exposure-total</b>	Cumulative Hg exposure from all pathways
<b>mehg-exposure-total</b>	Cumulative MeHg exposure from all pathways
<b>hg-exposure-total-normalized</b>	Normalized inorganic mercury exposure
<b>mehg-exposure-total-normalized previous-x (if not global)</b>	Normalized methylmercury exposure Previous x-location for travel-distance calculation
<b>previous-y (if not global)</b>	Previous y-location

## 9.4 Process Overview and Scheduling

1. Compute filtration capacity based on size, metabolism, and digestion efficiency.
2. Evaluate neighboring patches using a Gaussian suitability curve around optimal SPM.
3. Apply a competition penalty based on the number of con-specifics feeding on each patch.
4. Select the patch with the highest filtration benefit.
5. Move toward the chosen patch with travel distance reduced by swimming efficiency.
6. Apply swimming energy cost.
7. Filter feed by assimilating SPM scaled biomass from the chosen patch.
8. Assimilate mercury and methylmercury using biomagnification factors from Lavoie et al (2013).
9. Add assimilated biomass and contaminants to stomach contents.

## 9.5 Design Concepts

### Basic Principles

Filter feeding reflects how pelagic and estuarine fish forage on suspended par-

ticles while migrating. Filtration scales with size, metabolism, and digestive efficiency. SPM determines food availability and contaminant exposure.

#### **Emergence**

Feeding hotspots emerge where hydrodynamic SPM fields align with optimal SPM and competition is minimal. Contaminant loads emerge from local mercury and methylmercury concentrations and biomagnification.

#### **Adaptation**

Agents adjust their direction and feeding behavior based on SPM quality, filtration capacity, and local competition.

#### **Sensing**

Agents sense SPM, mercury, methylmercury, competition from conspecifics, stomach fullness, and their own metabolic and digestive state.

#### **Stochasticity**

Variation in SPM quality, contaminant concentrations, and local competition create variability in feeding and assimilation outcomes.

#### **Interaction**

Competition reduces filtration benefit when more fish feed on the same patch. Mercury and methylmercury assimilation depends on local contaminant levels and feeding intensity.

#### **Observation**

The model tracks biomass intake, mercury and methylmercury assimilation, stomach contents, and contaminant load added per patch.

## 9.6 Initialization

Variable	Initialized Value	Justification
stomach-contents	0	No biomass in the stomach at model start
stomach-contents-Hg	0	No initial inorganic mercury from feeding
stomach-contents-MeHg	0	No initial methylmercury
digestion-efficiency	Species specific	Determines fraction of filtered biomass assimilated
optimal-SPM	Species specific	Represents preferred SPM concentration

## 9.7 Submodels

### 9.7.1 Filtration Capacity

Filtration scales with size, metabolism, and digestion efficiency:

$$\text{Filtration}_{base} = \left( \frac{\text{size}}{100} \right) \cdot \text{metabolism\_rate} \cdot \text{digestion\_efficiency}$$

### 9.7.2 SPM Interest (Gaussian Suitability)

Suitability peaks at the optimal SPM and declines with distance:

$$\text{Interest} = e^{-\frac{(SPM - \text{optimal SPM})^2}{2 \cdot \sigma^2}}$$

Where  $\sigma$  is the SPM standard deviation tolerance (here 25).

### 9.7.3 Benefit Calculation

Benefit for each neighboring patch:

$$\text{Benefit} = SPM \cdot \text{Interest} \cdot \text{Filtration}_{base}$$

If con-specifics are present:

$$\text{Benefit} = \frac{\text{Benefit}}{N_{conspecifics}}$$

### 9.7.4 Movement

Travel distance is reduced by swimming efficiency:

$$\text{Distance} = \min(\text{DistanceToPatch}, \text{speed} \cdot \text{swim\_efficiency})$$

Energy cost of swimming:

$$\text{Energy} = \text{Energy} - (\text{E\_swim} \cdot \text{Distance})$$

### 9.7.5 Feeding and Stomach Loading

Assimilated biomass:

$$\text{Intake} = \min(\text{PreyAssimilated}, \text{StomachCapacity} - \text{StomachContents})$$

### 9.7.6 Contaminant Assimilation and Biomagnification

Biomagnification factors follow ?:

$$BMF_{MeHg} = 10^{(0.24 \cdot \Delta TP)}$$

$$BMF_{Hg} = 10^{(0.14 \cdot \Delta TP)}$$

With  $\Delta TP = 1$ :

$$BMF_{MeHg} = 10^{0.24} \approx 1.74$$

$$BMF_{Hg} = 10^{0.14} \approx 1.38$$

Assimilation equations:

$$MeHg_{assim} = SPM \cdot MeHg_{patch} \cdot BMF_{MeHg} \cdot \text{PreyAssimilated}$$

$$Hg_{assim} = SPM \cdot Hg_{patch} \cdot BMF_{Hg} \cdot \text{PreyAssimilated}$$

Stomach contaminant update:

$$StomachMeHg = StomachMeHg + MeHg_{assim}$$

$$StomachHg = StomachHg + Hg_{assim}$$

```

globals [
    ; Filter feeding parameters
    spm-sd           ;; standard deviation for Gaussian SPM preference curve (2
    max-filter-distance      ;; how far fish can evaluate patches (optional)

    ;; Biomagnification constants from Lavoie et al. 2013
    BMF-MeHg          ;; 1.74 (MeHg biomagnification factor)
    BMF-Hg            ;; 1.38 (Hg biomagnification factor)
]

patches-own [
    ; physical environment
    SPM                ;; suspended particulate matter
    patch-terrain       ;; "water" or "land"

    ; contaminant concentrations
    mercury           ;; inorganic Hg
    methylmercury      ;; MeHg
]

fish-own [
    ; -----
    ; Filter feeding physiology
    ; -----
    size               ;; body size scaling filtration
    metabolism-rate   ;; modulates filtration intensity
    digestion-efficiency  ;; fraction of filtered biomass digested
    optimal-SPM        ;; preferred SPM concentration
    filter-feed?        ;; Boolean: whether agent filter feeds

    ; -----
    ; Movement & energy
    ; -----
    speed              ;; movement rate
    swim-efficiency    ;; metabolism-adjusted efficiency
    E-swim             ;; energy cost per unit distance
    energy             ;; energetic budget

    ; -----
    ; Stomach contents
    ; -----
    stomach-contents
    stomach-capacity
    stomach-contents-Hg    ;; inorganic Hg from filter feeding
]

```

```

stomach-contents-MeHg      ;; MeHg from filter feeding

;; -----
;; Contamination physiology
;; (needed for risk integration)
;; -----
hg-total                  ;; cumulative Hg body burden
mehg-total                ;; cumulative MeHg body burden
hg-exposure-total
mehg-exposure-total
hg-exposure-total-normalized
mehg-exposure-total-normalized
]

to filter-feed
if filter-feed? [
  let spm-sd 25
  ;; Base filtration capacity scales with body size *and* metabolism
  let base-filtration ((weight / 100) * metabolism-rate)
  set base-filtration (base-filtration * digestion-efficiency)
  let neighbors-list sort (neighbors with [patch-terrain = "water"])
  let best-patch nobody
  let best-score -999

  foreach neighbors-list [p ->
    let spm-patch [SPM] of p
    let interest exp (- ((spm-patch - optimal-SPM) ^ 2) / (2 * (spm-sd ^ 2)))
    let benefit (spm-patch * interest * base-filtration)
    let comp count alewives-on p
    if comp > 0 [ set benefit benefit / comp ]
    if benefit > best-score [
      set best-score benefit
      set best-patch p
    ]
  ]
  if best-patch != nobody and [patch-terrain] of best-patch = "water" [
    face best-patch
    face best-patch
    move-to best-patch

    ;; calculate ditance between best patch and previous patch
    let travel-distance distancexy previous-x previous-y

    ;; --- Swimming energy cost (scaled by efficiency) ---
  ]
]

```

```

set energy max list 0 (energy - (E-swim * travel-distance))

;; --- Feeding and digestion (temperature-dependent) ---
let patch-spm [SPM] of best-patch
let prey-assimilated patch-spm * base-filtration * 300

;; --- Contaminant uptake (SPM × Hg and MeHg) ---
let spm-hg [mercury] of best-patch
let spm-mehg [methylmercury] of best-patch

;; --- Biomagnification ---
let biomag-factor (random-float 30) + 60 ;; random 60-90
let hg-assimilated (patch-spm * spm-mehg * biomag-factor * prey-assimilated)
let mehg-assimilated (patch-spm * spm-hg * (biomag-factor / 10) * prey-assimilated)

;; Remaining capacity
let space-available (stomach-capacity - stomach-contents)

;; You can only eat as much as fits
let intake (min (list prey-assimilated space-available))

;; Add biomass to stomach
set stomach-contents (stomach-contents + intake)
set stomach-contents-Hg (stomach-contents-Hg + hg-assimilated);; mercury stomach an
set stomach-contents-MeHg (stomach-contents-MeHg + mehg-assimilated);; methylmercu

]
end

```

## 9.8 Overview

Lipid catabolism provides a secondary energy pathway that fish use when immediate food resources are unavailable or when energy falls below a functional threshold. In this submodel, agents metabolize stored lipid reserves to restore energy, maintain migration, and avoid starvation. Lipid use is influenced by body condition, metabolic efficiency, and the magnitude of energetic deficit. Lipid depletion also reduces body weight over time, creating a biologically meaningful cost to sustained lipid reliance. Contaminant uptake does not occur during lipid catabolism, reflecting the absence of feeding.

## 9.9 Purpose

The purpose of this submodel is to simulate endogenous energy mobilization through lipid reserves when fish cannot meet energetic needs through feeding. Lipid catabolism allows migratory fish to continue movement and survive temporary periods of low food availability. This mechanism reflects empirical observations of lipid use during spawning migrations, overwintering, and other energetically demanding life history periods.

This submodel is best used in tandem with an energy recovery strategy like filter feeding and digestion, or predation and digestion.

## 9.10 Entities, State Variables, and Scales

### 9.10.1 Spatial and Temporal Scales

**Spatial Unit:** Patch (3 m x 3 m resolution)

**Temporal Unit:** 5 minute time steps (tick)

### 9.10.2 Global Variables

Global Variable	Definition
<b>full-energy-level</b>	Target energy level used to compute energetic deficit during lipid use (default = 100).
<b>energy-per-lipid</b>	Energy returned per unit lipid mass mobilized (default = 40), used to convert lipid into energy.
<b>lipid-refill-fraction</b>	Fraction of body mass available to mobilize as lipid during fasting (default = 0.5).
<b>lipid-max-fraction</b> ( <i>optional</i> )	Upper bound on lipid fraction that can be lost before mortality or physiological collapse (not currently enforced but biologically relevant).
<b>debug-lipid?</b> ( <i>optional</i> )	Toggles printing of intermediate lipid catabolism calculations for debugging.

### 9.10.3 Patch Variables

Lipid catabolism does not directly depend on patch level variables, since no external resources are consumed.

#### 9.10.4 Agent Variables

Variable Name	Definition
<b>energy</b>	Current energy level of the agent
<b>weight</b>	Current body mass of the fish
<b>original-weight</b>	Initial body mass used to scale maximum lipid availability
<b>lipid-catabolism-efficiency</b>	Efficiency with which lipids are converted into usable energy. This value is equal to the current metabolic rate divided by the metabolic rate at optimal temperature, allowing lipid use to scale with physiological performance
<b>lipid-used</b>	Amount of lipid converted to energy during the current step
<b>metabolism-rate</b>	Current metabolic rate, which influences efficiency scaling
baseline-metabolism-rate	Metabolic rate at optimal temperature
<b>mehg-foraging</b>	Methylmercury acquired during feeding (set to zero when lipids are used)
<b>hg-foraging</b>	Inorganic mercury acquired during feeding (set to zero when lipids are used)
<b>mehg-foraging-total</b>	Total methylmercury obtained from foraging
<b>hg-foraging-total</b>	Total inorganic mercury obtained from foraging
<b>mehg-total</b>	Total methylmercury accumulated
<b>hg-total</b>	Total inorganic mercury accumulated

### 9.11 Process Overview and Scheduling

1. Compute energy deficit relative to a target energy level of one hundred.
2. Determine the lipid amount needed to fill the deficit.
3. Limit lipid use by the maximum lipid available for mobilization.
4. Apply lipid catabolism efficiency to determine usable lipid energy.

5. Convert mobilized lipid to energy.
6. Reduce weight by the amount of lipid burned.
7. Set contaminant uptake to zero during this process, since no feeding occurs.

## 9.12 Design Concepts

### **Basic Principles**

Lipid catabolism models endogenous energy mobilization in the absence of food. Fish draw upon lipid stores when energy is low, which is a well documented physiological process during migration, overwintering, and fasting.

### **Emergence**

Patterns of weight loss, energy cycling, and recovery emerge from repeated lipid use during periods of limited food access.

### **Adaptation**

Agents adaptively mobilize lipids based on the severity of their energy deficit and on efficiency scaling from the metabolism submodel.

### **Objectives**

Agents seek to maintain enough energy to migrate, forage, avoid predation, and prevent starvation.

### **Sensing**

Agents sense their own internal energy level and lipid reserve availability.

### **Interaction**

Lipid catabolism does not require environmental interaction and therefore represents a purely endogenous process.

### **Stochasticity**

This submodel is deterministic. However, variation in weight, metabolism, and previous feeding creates emergent differences among individuals.

### **Observation**

Outputs include energy restored through lipid catabolism, lipid used, and body mass loss over time.

## 9.13 Initialization

Variable	Initialized Value	Justification
weight	species specific	Establishes initial body condition
original-weight	equal to initial weight	Defines total lipid availability
energy	100	Full energy at initialization
lipid-catabolism-efficiency	from metabolism submodel	Reflects physiological scaling of lipid use
lipid-used	0	No lipid used at start

## 9.14 Submodels

### 9.14.1 Lipid Mobilization

Maximum lipid available for mobilization depends on relative body mass:

$$Lipid_{refill} = 0.5 \times \left( \frac{weight}{original\_weight} \right)$$

Energy deficit relative to full energy:

$$Energy_{deficit} = 100 - Energy$$

Lipid required to refill the deficit:

$$Lipid_{needed} = \frac{Energy_{deficit}}{40}$$

Actual lipid mobilized:

$$Lipid_{used} = \min(Lipid_{needed}, Lipid_{refill}) \times lipid\_catabolism\_efficiency$$

### 9.14.2 Energy Conversion

Mobilized lipid is converted into energy:

$$Energy_{added} = Lipid_{used} \times 40$$

Energy is capped at one hundred:

$$Energy = \min(100, Energy + Energy_{added})$$

### 9.14.3 Weight Loss

Weight decreases proportionally to lipid used:

$$Weight = Weight - Lipid_{used}$$

### 9.14.4 Contaminant Bookkeeping

No mercury or methylmercury is acquired during lipid catabolism:

$$MeHg_{digested} = 0$$

$$Hg_{digested} = 0$$

These values are added to cumulative totals to maintain bookkeeping consistency, but do not increase contaminant burden.

## 9.15 Netlogo Implementation

```
;; =====
;; LIPID CATABOLISM SUBMODEL DECLARATIONS
;; =====

turtles-own [
    ;; Energetics & body condition
    energy
    weight
    original-weight

    ;; Lipid metabolism
    lipid-catabolism-efficiency
    lipid-used

    ;; Metabolic rate inputs
    metabolism-rate
    baseline-metabolism-rate

    ;; Contaminant bookkeeping during fasting
    mehg-foraging]
```

```

hg-foraging

mehg-foraging-total
hg-foraging-total

mehg-total
hg-total
]

;; =====
;; LIPID CATABOLISM SUBMODEL
;; =====

to lipid-loss
  ;; Maximum lipid metabolized this step, adjusted by efficiency
  let lipid-refill 0.5 * (weight / original-weight)
  ;print (word "lipid-refill: " lipid-refill)
  ;print (word "current energy: " energy)
  ;; Calculate deficit and lipid need
  let energy-deficit (100 - energy)
  ;print (word "energy-deficit: " energy-deficit)
  let lipid-needed (energy-deficit / 40)
  ;print (word "lipid-needed: " lipid-needed)

  ;; Actual lipid use depends on efficiency and availability
  let lipid-used (min list lipid-needed lipid-refill)
  set lipid-used (lipid-used * lipid-catabolism-efficiency)
  ;print (word "lipid-used: " lipid-used)

  ;; Convert lipid to energy (scaled by efficiency)
  let energy-change (lipid-used * 40)
  ;print (word "energy added: " energy-change)
  set energy (energy + energy-change)
  ;print (word "energy after lipid conversion: " energy)
  if energy > 100 [
    set energy 100
    print "energy capped at 100"
  ]

  ;; Weight loss proportional to lipid burned
  set weight weight - (lipid-used)
  ;print (word "weight after lipid loss: " weight)

  ;; When relying on lipids, Hg mercury foraging risk stops

```

```
;; contaminant bookkeeping
let digested-MeHg 0
let digested-Hg 0
set mehg-foraging digested-MeHg
set hg-foraging digested-Hg

set mehg-foraging-total mehg-foraging-total + digested-MeHg
set hg-foraging-total hg-foraging-total + digested-Hg
set mehg-total mehg-total + digested-MeHg
set hg-total hg-total + digested-Hg
end
```



# Chapter 10

## Landward Migration

### 10.1 Overview

This function simulates landward migration for fish moving upstream through riverine and estuarine systems. Agents adjust their movement based on local water velocity, energetic condition, and the relative difficulty of swimming in a given flow. Movement occurs along a least cost path that is recalculated according to hydrodynamic conditions.

### 10.2 Purpose

The purpose of this submodel is to represent upstream migration under realistic spatial hydrodynamic resistance. Agents evaluate flow velocity, movement difficulty, body condition, and patch level travel costs before advancing along a least cost path toward a home location.

### 10.3 Entities, State Variables, and Scales

#### 10.3.1 Spatial and Temporal Scales

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

#### 10.3.2 Global Variables

Variable	Definition
<b>max-seaward-velocity</b>	Maximum seaward directed velocity in the domain, used for normalization.
<b>max-landward-velocity</b>	Maximum landward directed velocity in the domain.

### 10.3.3 Patch Variables

Variable	Definition
<b>velocity</b>	Depth averaged hydrodynamic velocity at the patch.
<b>depth</b>	Water depth at the patch.
<b>patch-terrain</b>	Indicates whether the patch is water or land.
<b>cost-to-home</b>	Patch level cost field producing a least cost corridor.
<b>visits-by-alewife</b>	Number of times the agent visits the patch.
<b>ticks-spent-alewife</b>	Time spent on the patch.

### 10.3.4 Agent Variables

Variable	Definition
<b>weight</b>	Body mass of the fish.
<b>speed</b>	Current swimming speed.
<b>prev-speed</b>	Previous time step swimming speed.
<b>max-speed</b>	Maximum sustained speed.
<b>min-speed</b>	Minimum allowable speed.
<b>swim-efficiency</b>	Scaling factor for acceleration and deceleration.
<b>difficulty-factor</b>	Difficulty of movement under local velocity conditions.
<b>planned-path</b>	Sequence of patches in the least cost route.
<b>home-patch</b>	Destination patch for migration.
<b>trail</b>	Record of patches visited by the agent.

## 10.4 Process Overview and Scheduling

1. Compute swimming difficulty from hydrodynamic velocity and body size.
2. Calculate swimming speed using desired-speed, velocity influence, and acceleration limits.
3. Evaluate the least cost field and construct a path to the home patch.
4. Move along the path for a distance proportional to swimming speed.
5. Record patch visitation and time spent.

## 10.5 Design Concepts

### Basic Principles

Hydrodynamic constraints, difficulty scaling, and body condition influence agent movement.

### Emergence

Migration routes, temporal occupancy, and movement speed emerge from repeated interactions of flow and difficulty.

### Objectives

Agents attempt to reach the home patch but do not optimize globally. Movement follows the least cost route at each step.

### Sensing

Agents sense velocity and depth of the local and neighboring patches.

### Observation

Paths, timing, and residency can be monitored chronologically.

## 10.6 Initialization

Variable	Initial Value	Justification
<b>velocity</b>	user-defined	Hydrodynamic input data.
<b>weight</b>	species-specific	Required for difficulty scaling.
<b>max-speed</b>	species-specific	Physiological constraint.
<b>min-speed</b>	species-specific	Prevents speed collapse.

Variable	Initial Value	Justification
<b>swim-efficiency</b>	species or constant	Controls acceleration rate.
<b>difficulty-factor</b>	1	Neutral starting difficulty.
<b>prev-speed</b>	starting speed	Smooth initial movement.

## 10.7 Submodels

### 10.7.1 Swimming Difficulty

Swimming difficulty reflects the hydrodynamic effort required for the agent to move through its current patch. Velocity is normalized between the maximum observed landward and seaward velocities:

$$V_{\text{norm}} = \frac{V_{\text{patch}} - V_{\min}}{V_{\max} - V_{\min}}$$

This normalized velocity is scaled by relative body size  $M_{\text{agent}}/M_{\max}$  and raised to a scaling exponent  $k$ :

$$Df_{\text{raw}} = \left( \frac{V_{\text{norm}}}{M_{\text{agent}}/M_{\max}} \right)^k$$

Difficulty is then mapped onto the one to ten range:

$$D_f = 1 + 9 \cdot Df_{\text{raw}}$$

and constrained:

$$D_f \in [1, 10]$$

Difficulty increases when:

- $M_{\text{agent}}$  is small
- $|V_{\text{patch}}|$  approaches its maximum value
- flow opposes movement