SPelAgent - Model Overview - ODD protocol

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Contents

The `SPelAgent` simulates the population dynamics of European pilchard (*Sardina pilchardus*) and European anchovy (*Engraulis encransicolus*) using an agent-based framework informed by Dynamic Energy Budget (DEB) theory (Kooijman, 2009). This approach enables a mechanistic representation of individual energy acquisition and allocation throughout the life cycle—from egg masses to juveniles and adults—while capturing emergent population-level patterns such as biomass fluctuations, recruitment, and mortality (Martin et al., 2012).

SPelAgent is implemented in Julia (Bezanson et al., 2017), using the high-performance Agents.jl library, which offers superior computational efficiency compared to other platforms commonly used for agent-based modeling (Datseris et al., 2024). The model builds upon the individual-based model (IBM) developed by Haberle et al. (2023), but has been specifically adapted to reflect the biology of sardine and anchovy species and scale-up to realistic population dynamics simulation. The model investigates how environmental conditions (e.g., temperature, food availability), density dependence, and age-specific mortality interact with intrinsic biological processes (growth, reproduction, survival) at the individual level, to eventually shape population structure. Anthropogenic pressures, specifically fishing mortality, are also included to evaluate their impact on population dynamics.

In SPelAgent, the agent is a group of functionally identical fish (individuals) born on the same day - a *SuperIndividual (SIs)*. The use of agents as SIs ensure computational efficiency while maintaining ecological realism: the model performs bioenergetic computations at the superindividual level, making large-scale simulations feasible without compromising biological details (Scheffer et al., 1995; Rose et al., 2015). Each SI progresses through three life stages: **egg**, **juvenile**, and **adult**. Superindividuals are respectively called `:EggMass` (a superindividuals made of egg batches released from different adults), `:Juvenile` and `:Adult`. The model runs at a daily time step and it is not spatially explicit: the model simulates processes within the upper 200 meters of the water column, the core habitat for both species. In this protocol, the term *agent* refers to the entities on which model calculations are performed. In `SPelAgent`, these correspond to the superindividuals of type `:EggMass`, `:Juvenile`, and `:Adult`. By contrast, the term *individuals* denotes the single fish represented within each superindividual.

Environmental drivers (section 3.2.1) include daily temperature and food availability, which can be obtained from regional physical and biogeochemical reanalysis. In SPelAgent, food is defined as the integrated zooplankton biomass (expressed as $\frac{mgC}{m^2}$, in the upper 200 m, converted in Joules. Both temperature and food availability affect energy fluxes according to DEB theory (see Section 2.3 for DEB formulation).

All agents undergo core processes for aging, energy assimilation and allocation, and mortality (see 2.2). Mortality (section 3.3.1) may result from natural causes (predation and aging), fishing, or starvation, and is modulated by life stage, age, and environmental conditions. A

fixed egg mortality rate (99.98%) is applied prior to hatching (section 3.3.3)(Haberle et al., 2023).

Life stage–specific processes include hatching for egg masses, maturation for juveniles, and reproduction for adults (see section 3.3). Spawning occurs within a defined reproductive window, and batch size depends on adult weight, energy reserves, and batch fecundity (see section 3.3.6). At each time step, surviving agents go to the next timestep, the environment is refreshed, and dead individuals are removed from the simulation (section 3.4.1).

Daily outputs (section 3.4.2) include individual-level states (see Table 1) and population-level metrics (e.g., biomass, mortality by cause, individual reproductive success). Stochasticity (section 2.3, 3.3.6) is introduced through variability in key DEB parameters, maturation thresholds, and reproductive success, enhancing realism and capturing natural variation in sardine and anchovy populations.

The model is documented using the *ODD* (Overview, Design Concepts, and Details) protocol (Grimm *et al.*, 2010, 2020), a standardized framework for agent-based model description. ODD provides a structured, transparent way to present the model's purpose, underlying mechanisms, and implementation details, facilitating reproducibility and comparative analysis across studies.

1 Overview

1.1 Purpose

The model simulates the population dynamics of sardine and anchovy using SuperIndividuals (SIs) agents, focusing on energy allocation, life-history transitions, and population-level interactions under the framework of Dynamic Energy Budget (DEB) theory. Its goal is to investigate how environmental factors (e.g., temperature, food availability), fishing pressure, and intrinsic biological processes (e.g., growth, reproduction, natural mortality) influence the demography and life-history traits of sardine and anchovy populations.

1.2 Entities, State Variables, and Scales

1.2.1 Entities and State Variables

- **Agent** The `SPelAgent` model currently supports simulations for either sardine or anchovy independently. The primary entities in the model are sardine or anchovy SuperIndividuals (SIs), defined as cohorts of functionally identical individuals born on the same day. Each SI comprises both sexes, assuming a 1:1 sex ratio. SIs can belong to one of the following life stages:

- **Egg**: The SI is coded as `:EggMass` and represents a collection of egg batches spawned from multiple adults on the same day (see section 3.3.6).

- **Juvenile**: The SI is coded as `:Juvenile` and represents individuals survived to hatching, up to the onset of maturity.

- **Adult**: The SI is coded as `:Adult` and represents mature individuals capable of reproduction.

All SIs attributes are defined in Table 1.

- **Environment** The model environment is a homogeneous water column representing the upper 200 meters, which is the primary habitat of both species. It is described by the average water temperature (°C) and food availability, as the total zooplankton available expressed in Joules. Conversion from $mgCm^{-2}$, the typical output of biogeochemical reanalysis, is possible assuming that 1g of carbon is equal to 46 kJ (Salonen et al., 1976; Postel et al., 2000)

Table 1: Description of individual-level attributes in SPelAgent.

Key	Definition
type	The life stage of the sardine: `:EggMass`, `:Juvenile`, or `:Adult`.
reproduction	Indicates whether the fish is a spawner or not: `:spawner`, `:nonspawner`.
Nind	Number of individuals at the timestep in the superindividual group.
Nind0	Number of individuals when the superindividual is initialized.
Age	The age of the fish in days.
L	Structural length of the sardine. This is assumed to be close to zero for eggs according to DEB Theory.
H	Maturation state variable.
maternal_EggEn	Energy of the egg due to maternal effects (E0).
superind_Neggs	Number of eggs produced by a superindividual.
En	Reserve energy state variable.

Key	Definition
`Dead`	Indicates if the sardine is dead (`true`) or alive (`false`).
`Death_type`	*natural* if `N_ind` falls below the death threshold due to natural or fishing mortality, or *starved* otherwise.
`f_i`	Individual functional response. Applicable for juveniles and adults and derived from the communal functional response.
`t_puberty`	Time to reach puberty. Fixed once matured.
`Lw`	Physical length (real in cm).
`Ww`	Total weight of the fish.
`Wg`	Gonads weight of the fish.
`R`	Reproduction state variable. Positive for adults, set to 0 otherwise.
`Scaled_En`	Scaled energy reserve density, equal to $[E]/[E_m] = \frac{E/V}{\{\dot{p}_{Am}\}\dot{v}}$
`s_M_i`	Individual acceleration factor s_M of abj model.
`pA`	Realized individual assimilation at timestep $\dot{p}_A$.
`pAm_i`	Individual specific max assimilation rate $\{\dot{p}_{Am}\}$.
`pXm_i`	Individual specific max ingestion rate.
`pM_i`	Individual specific maintenance rate $[\dot{p}_M]$.
`Hp_i`	Individual specific energy threshold to puberty E_H^p.
`Hj_i`	Individual specific energy threshold to metamorphosis E_H^j.
`Hb_i`	Individual specific energy threshold to birth E_H^b.
`K_i`	Individual specific allocation fraction to soma κ.
`Lm_i`	Individual specific maximum length L_m.
`Em_i`	Individual specific maximum reserve density $[E_m]$.
`g_i`	Individual specific energy investment ration g.
`k_M_i`	Individual specific somatic maintenance rate coefficient $\dot{\kappa}_M$.
`zoom_i`	Individual specific zoom factor.
`Lb_i`	Length at birth for the individuals. Structural.
`Lj_i`	Length at metamorphosis for the individual. Structural.
`CI`	Condition Index.

Key	Definition
GSI	Gonadosomatic Index.
dryGSI	Gonadosomatic Index based on dry weight of gonads to avoid overestimation.
spawned	Number of times the sardine has spawned. Applicable to adults.

1.2.2 Scales

- **Temporal**: Daily time step.

- **Spatial**: Implicit; homogeneous environment in the 0–200 m water column.

2 Design concepts: Process Overview and Scheduling

2.1 Initialization

The `model_initialize()` function sets the initial population structure and environmental conditions. It requires the number of superindividuals that should be initialized for each lifestage, environmental time series (temperature and food), and mortality rates for age classes 0+ to 4+. Boolean flags activate mechanisms such as DEB parameter inheritance (see 3.3.6), weighted inheritance by fecundity, thinning mortality (see 3.3.1), covariation between $\{\dot{p}_{Am}\}$ and E_H^p, and size- or age-based fishing selectivity. More details in Section 3.1.

2.2 Processes and Scheduling

Each simulation step represents one day and follows a defined sequence of operations involving both agents and the environment. At the beginning of each day, output variables are reset to zero to save outputs at a daily temporal resolution and not cumulatively. Agents flagged as dead are removed from the population, while surviving agents proceed through life-stage-specific submodels. The model decision flow chart is shown in Fig 1.

:`EggMass` undergo aging, DEB-based energy allocation, and hatching when the maturation threshold is reached, with a fixed pre-hatching mortality of 99.98%, similarly to Haberle et al. (2023).

:Juveniles experience natural mortality, starvation, and—if longer than 10 cm, fishing mortality. Energy is assimilated and allocated according to DEB theory into maintenance, growth, and maturation. If enough energy is stored in the maturity state variable, they become adults.

:Adults are subject to the same mortality types. Energy is allocated to maintenance, growth, and reproduction. Adults spawning during a species-specific reproductive window are flagged as :spawner: all the eggs released by the spawners, on the same day, are collected into a new SuperIndividual (SI), whose initial number of individuals (Nind0) is equal to the number of eggs simultaneously released. If inheritance is active, offspring inherit DEB parameters based on parental traits, optionally weighted by egg contribution.

At the end of each day, population-level outputs are collected, including population biomass and abundance, total deaths by cause and stage, and mean individual traits. Environmental variables, temperature (Tc) and food availability (X_{tot}), are updated from input time series. More details are provided in Sections 3.3 and 3.4.
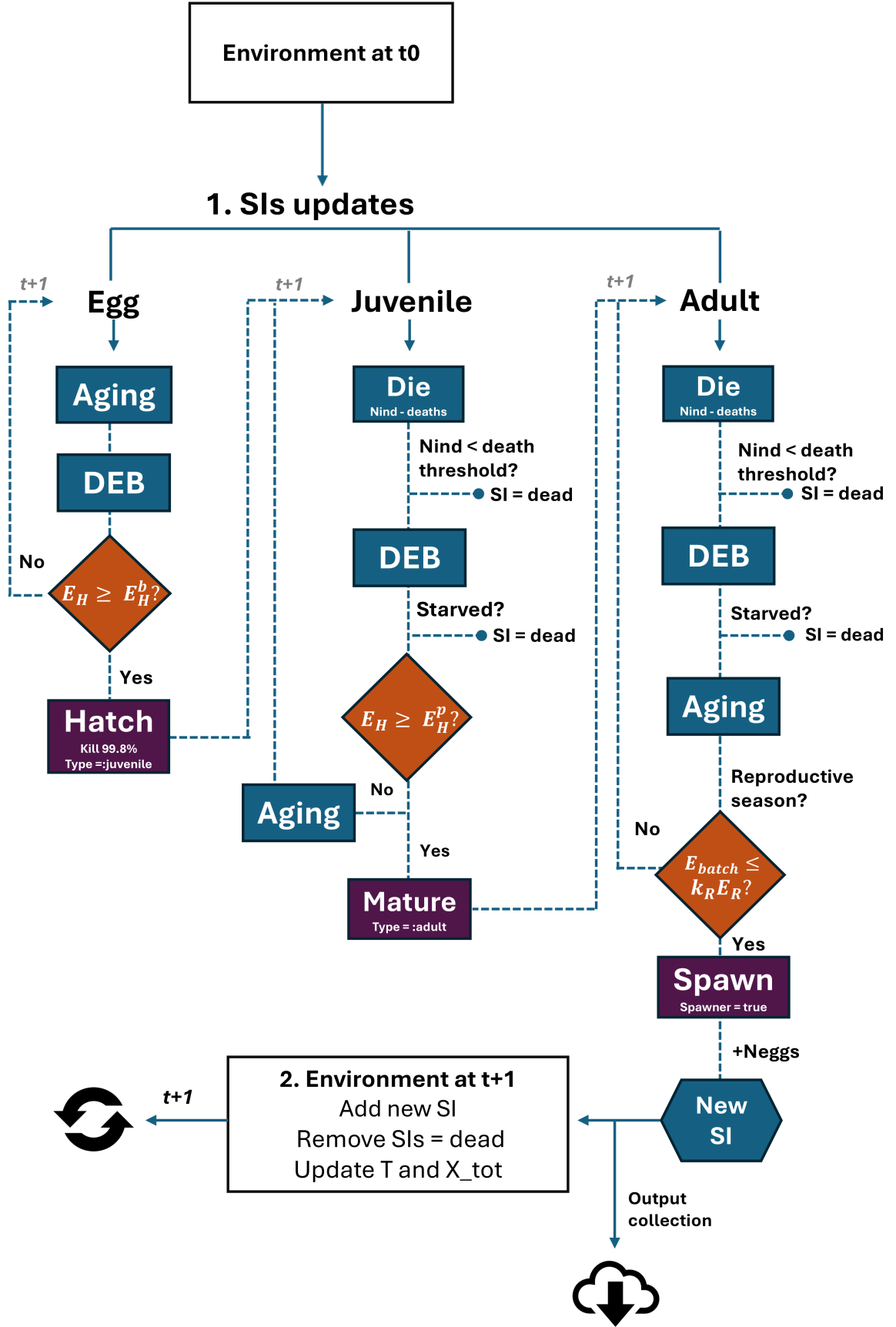
Figure 1: SPelAgent daily timestep scheduling

2.3 Design Concepts

Basic Principles The model is grounded in the Dynamic Energy Budget (DEB) theory (Kooijman, 2009; Nisbet et al., 2012; Van Der Meer, 2006), which describes how organisms assimilate energy from their environment and allocate it to maintenance, growth, maturation, and reproduction. Life-stage-specific processes are explicitly represented, with transitions from egg to juvenile (birth) and from juvenile to adult (puberty) driven by maturation thresholds and energy dynamics. In DEB, the physical length of an organism (Lw, measurable) is related to the individual structural length L by a shape parameter δ_M, so that:

$$L_w = \frac{L}{\delta_M} \tag{1}$$

The structural length is used in DEB equations and quantifies the structural body of the organism, $V = L^3$. All energetic processes are related to V: energy acquisition is proportional to the body surface ($V^{2/3}$ or L^2, for isomorphy, see paragraph 2.3 "DEB Model Variant: abj") while metabolic demands depend mostly on volume (V or L^3). Structure V is the first of the four main state variables in the standard DEB model:

- **Structural volume** V [cm^3], representing the organism's physical biomass, which determines its body size (length) and requires maintenance. It is calculated as the structural length of the organism to the power of 3 (L^3). It contributes to the total body weight.

- **Reserve energy** E [J], the assimilated energy stored in a generalized pool that can be mobilized to support metabolism and buffer starvation during periods of limited food availability. It doesn't require maintenance but contributes to body weight.

- **Maturity energy** E_H [J], the cumulative energy invested into development, which drives ontogenetic transitions. It requires maintenance, but do not contribute to body weight. After puberty $E_H = E_H^p$.

- **Reproduction buffer** E_R [J], starts wehn $E_H \geq E_H^p$: the energy allocated to reproduction after maturation is complete, typically associated with gonadal development and egg production. It contributes to body weight.

Transitions between life stages are governed by E_H: individuals are considered *born* (juvenile) when $E_H \geq E_H^b$ and reach *puberty* (adult and capable of reproducing) when $E_H \geq E_H^p$. After puberty, E_H remains constant at $E_H = E_H^p$.

The DEB framework defines energy fluxes (in units of J day^{-1}) among compartments. The main fluxes include:

- **Ingestion flux $\dot{p}_A$**: the rate at which food is ingested. This flux is proportional to the organism's surface area (L^2 or $V^{2/3}$), to the species-specific maximum ingestion rate per unit of surface area $\{\dot{J}_{Xm}\}$, and to the food availability via a scaled functional response:

$$f = \frac{X}{X_K + X} \tag{2}$$

where X is the food density in the environment, and X_K is the half-saturation coefficient (i.e., the food density at which the ingestion rate is half its maximum). Then, the ingestion flux is:

$$\dot{J}_X = f\,\{\dot{J}_{Xm}\}L^2 \tag{3}$$

- **Assimilation flux $\dot{p}_A$**: the rate at which ingested energy is stored in the reserve pool. This flux is equal to the ingestion flux multiplied by a conversion efficiency coefficient $k_X = \{\dot{p}_{Am}\}/\{\dot{J}_{Xm}\}$. Then:

$$\dot{p}_A = \dot{J}_X\,k_X = f\,\{\dot{J}_{Xm}\}\frac{\{\dot{p}_{Am}\}}{\{\dot{J}_{Xm}\}}L^2 = f\{\dot{p}_{Am}\}L^2 \tag{4}$$

The assimilation flux is proportional to the organism's surface area (L^2 or $V^{2/3}$) and to the food availability via the scaled functional response f.

In this model, only the assimilation flux is explicitly modelled, and we incorporate density dependence using the *communal functional response* introduced by Haberle et al. (2023); see Section 3.4 for details.

- **Mobilization flux $\dot{p}_C$**: the energy mobilized from the reserve pool to meet metabolic demands.

  A fixed fraction κ of $\dot{p}_C$ is allocated to the *somatic branch*, consisting of:

  - **Somatic maintenance flux $\dot{p}_S \propto V$** (i.e., L^3)

  - **Growth flux $\dot{p}_G$**, increasing the structural volume V

  The remaining energy $(1 - \kappa)\dot{p}_C$ is directed to the *maturity/reproduction branch*:

  - **Maturity maintenance flux $\dot{p}_J$**

  - **Maturation or reproduction flux $\dot{p}_R$**

The mobilization flux is equal to:

$$\dot{p}_C = E\frac{[E_G]\dot{v}V^{2/3} + \dot{p}_s}{\kappa E + [E_G]V} \tag{5}$$

where E is the reserve, $[Eg]$ the cost per unit of structure ($\mathrm{cm\,day^{-1}}$), $\dot{v}$ the energy conductance ($\mathrm{J\,cm^{-3}}$) and V the structural volume.

Note that assimilation and ingestion are processes associated with exogenous feeding, which occurs only in juveniles and adults. In contrast, eggs rely solely on the mobilization of energy from maternal reserves provided at the time of spawning. See section 3.3.6.

The κ partitioning makes growth and reproduction only indirectly in competition, as the allocation is fixed by κ. However, since $\dot{p}_A$ scales with surface area (L^2), smaller individuals assimilate less, limiting the energy available for mobilization, and ultimately for reproduction.

In juveniles, $\dot{p}_R$ is first used to cover $\dot{p}_J$; any surplus increases E_H. In adults, E_H no longer increases, and the surplus energy is stored in the reproductive buffer E_R.

It is important to note that:

- Assimilation depends on the surface area ($\propto L^2$)

- Somatic maintenance depends on the volume ($\propto L^3$)

State variables and fluxes equations are shown in Tab. 2 and in Fig. 2, while core primary parameters of the standard DEB model are shown in Tab. 3.

Table 2: State variables, dynamics, and energy fluxes

State Variable and Dynamics	Energy Fluxes
E: reserve energy	$\dot{p}_A = \{\dot{p}_{Am}\}fV^{2/3}$
V: structural volume	$\dot{p}_C = E\left(\dfrac{[E_G]\dot{v}V^{2/3} + \dot{p}_s}{\kappa E + [E_G]V}\right)$
E_H: maturity	$\dot{p}_S = [\dot{p}_M]V$
E_R: reproduction buffer energy	$\dot{p}_G = \kappa\dot{p}_C - \dot{p}_S$
$\dfrac{dE}{dt} = \dot{p}_A - \dot{p}_C$	$\dot{p}_J = \dot{k}_J E_H$
$\dfrac{dV}{dt} = \dfrac{\dot{p}_G}{[E_G]}$	$\dot{p}_R = (1-\kappa)\dot{p}_C - \dot{p}_J$
$\dfrac{dE_H}{dt} = p_R \quad (E_H < E_H^p)$	
$\dfrac{dE_R}{dt} = k_R\dot{p}_R \quad (E_H \geq E_H^p)$	

Table 3: The 12 primary parameters of the standard DEB model, shown in both a time–length–energy and a time–length–mass framework. Units: e in J, t in day^{-1}, L in cm. The parameter $\{\dot{p}_T\}$ is not used for marine ectotherms.

Symbol	Dimension (time–length–energy)	Description
$\{\dot{F}_m\}$	$L^2 t^{-1}$	Specific searching rate
$\{\dot{p}_{Am}\}$	$eL^{-2}t^{-1}$	max spec. assimilation rate
κ_X	—	Assimilation efficiency
$\dot{v}$	Lt^{-1}	Energy conductance
κ	—	Allocation fraction to soma
κ_R	—	Reproduction efficiency
$[\dot{p}_M]$	$eL^{-3}t^{-1}$	Volume-specific som. maint. cost
$\dot{k}_j$	t^{-1}	maturity maintenance rate coefficient
$[E_G]$	eL^{-3}	Specific cost for structure
E_H^b	e	Maturity at birth
E_H^p	e	Maturity at puberty
$\{\dot{p}_T\}$	$eL^{-2}t^{-}1$	Surface-specific maintenance cost

Temperature Correction   All metabolic rates are corrected for environmental temperature using the Arrhenius correction:

$$T_c = \exp\left(\frac{T_A}{T_r} - \frac{T_A}{T} \right) \tag{6}$$

where:

- T_A: Arrhenius temperature (K), a species-specific constant

- T_r: reference temperature, set to $293\,\mathrm{K}$ (20°C), at which DEB parameters are calculated

- T: current temperature (K)

While temperature accelerates physiological rates, it does not affect asymptotic size or size at maturity. The higher the value of T_A, the greater the species' sensitivity to temperature (Lika et al., 2011).

DEB Model Variant: `abj` Model for Fish   The standard DEB model assumes isomorphy of the organism throughout life ($Area \propto V^{2/3}$). However, sardine and anchovy are modeled using a typified DEB model, the `abj` model, which incorporates a temporary phase of metabolic acceleration, where the organism is considered a V1-morph ($Area \propto V$; Kooijman et al. 2011, 2014, Marques et al. 2018).

This **acceleration model** introduces an additional life stage transition — *metamorphosis* —occurring between birth and puberty, when $E_H^b \leq E_H \leq E_H^j$. In this transition the individual is a V1 morph, while before and after, an isomorph.
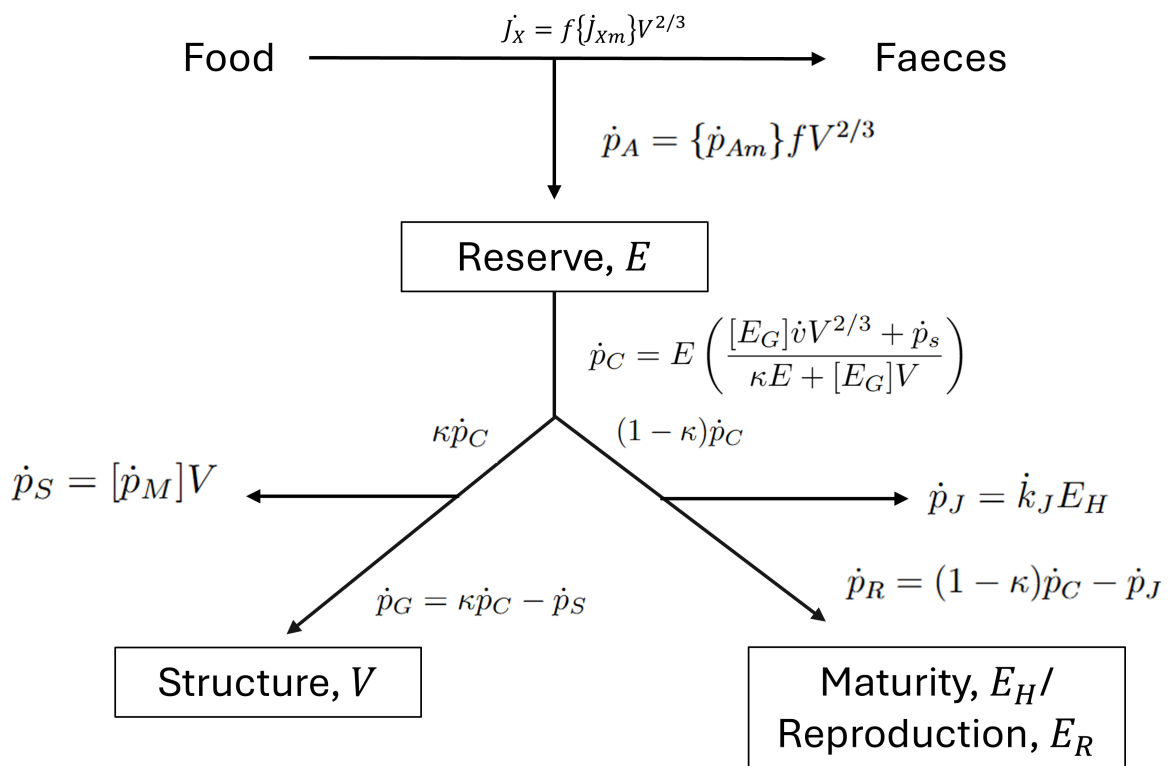
Figure 2: Standard DEB model state variables and fluxes

The `abj` model extends the standard DEB model with a single additional parameter, the **acceleration factor** s_M. The $\{\dot{p}_{Am}\}$ and $\dot{v}$ parameters are multiplied by s_M to reflect the increased assimilation and mobilization rates during the metamorphosis of the fish (V1 morph). This allows for faster growth during early juvenile stages, reflecting biological observations in many fish species.

Before birth s_M is set to 1; during metamorphosis ($E_H^b \leq E_H \leq E_H^j$), $s_M = \dfrac{L_w \cdot \delta_M}{L_b}$; after metamorphosis, $s_M = \dfrac{L_j}{L_b}$.

Emergence   Population-level phenomena such as biomass dynamics, age structure, and reproductive success emerge from the aggregation of individual-level processes and their interactions with a dynamic environment.

Adaptation   Agents dynamically adjust their energy allocation depending on environmental conditions, particularly temperature and food availability, but are not capable of learning or goal-seeking behavior.

Objectives   Agents do not pursue explicit goals; their behavior is determined by physiological rules embedded in DEB.

Learning   No learning mechanism is implemented.

Prediction   Agents do not predict future environmental conditions. They respond dynamically to their current physiological state and local environmental variables.

Sensing   Agents sense food availability and competition for food via the communal functional response (f_{comm}, Section 3.4.1). Temperature influences all metabolic rates (see Section 2.3).

Interaction   Agents interact indirectly through resource competition. Food availability is shared and influences individual assimilation rates via the communal functional response (3.4.1).

Stochasticity   Stochastic variation is incorporated into several biological traits and processes to reflect natural variability observed in real populations:

- **Maturation energy threshold (E_H^p) and somatic maintenance rate coefficient ($[\dot{p}_M]$)**: sampled from a normal distribution centered on the estimated parameters with a standard deviation of 0.1, to avoid juvenile-driven cycles (Kooijman 2024; see Section 3.1.1).

- **Reproduction-related traits:** stochasticity affects spawning onset, individual fecundity, and reproductive efficiency (see Section 3.3.6 for details).

Stochasticity is also applied during agent initialization (Section 3.1.1): if not specified, individual structural length is randomly sampled from a biologically realistic distribution centered on the mean length for juveniles or adults, drawn from the literature.

Mortality processes are modeled as stochastic events: at each time step, the number of deaths is determined by drawing from a binomial distribution, incorporating age-specific and environmentally driven mortality probabilities (see Section 3.3.1).

3 Details

3.1 Initialization

A simulation is initialized through the `model_initialize()` function, which defines the starting conditions for both the population and the environment. A set of boolean inputs controls the activation of key biological and ecological mechanisms:

- `inheritance`: Enables inheritance of selected DEB parameters from parents to offspring (see Section 3.1.1).

- `weight`: Weights inheritance by the number of eggs each SI produces (see Section 3.1.1).

- `thinning`: If true, applies additional mortality to juveniles, to prevent density-driven juvenile cycles (Kooijman 2024; see Subsection 3.3.1).

- `zoom`: Activates covariation between $\{\dot{p}_{Am}\}$ and E_H^p, scaled by a zoom factor (Lika et al. 2011; see Section 3.1.1).

The user must provide the initial number of SIs in each life stage and the starting day of the year. Environmental drivers—daily time series of temperature (°C) and food availability (J)—must cover the entire simulation period. Additionally, stage-specific natural and fishing mortality rates for age classes 0+ to 4+ are required.

3.1.1 Agent Initialization

The `generate_()` family of functions creates the specified number of superindividuals of a given type (`:Adult`, `:Juvenile`, or `:EggMass`) and initializes their biological and DEB-related properties (Table 1). These properties include length, weight, age, and key DEB parameters. The initial values of DEB state variables are set to be consistent with DEB theory. For example,

juveniles start with a reproduction buffer $E_R = 0$, and maturity energy is set to $E_H = E_H^p$ for adults.

Parameter Initialization: Inheritance vs. No Inheritance Simulations Each agent receives individualized DEB parameters depending on whether inheritance is enabled:

- **No Inheritance:** stochastic variation is introduced only in E_H^p and $[\dot{p}_M]$ to prevent the emergence of strong juvenile-driven population cycles, as recommended by Kooijman (2024). All other parameters remain fixed across individuals.

$$E_{H,i}^p = E_H^p \cdot \exp(\mathcal{N}(0, 0.1)) \tag{7}$$

$$[\dot{p}_{M,i}] = [\dot{p}_M] \cdot \exp(\mathcal{N}(0, 0.1)) \tag{8}$$

- **Inheritance Enabled:** inter-individual variability is introduced in $[\dot{p}_M]$, $\{\dot{p}_{Am}\}$, and E_H^p to investigate the evolution of life-history traits. Two modes of inheritance are supported:

  - **With Zoom Factor:** parameters $\{\dot{p}_{Am}\}$ and E_H^p covary via a shared zoom factor $z_i \sim \mathcal{N}(1, 0.066)$ (Lika et al., 2011). This indicates that 99.7% of the population has a zoom factor within $\pm 20\%$ of the mean (set at 1, corresponding to the original individual; Menu 2024). The maintenance coefficient $[\dot{p}_M]$ is drawn independently from a normal distribution centered in the DEB standard parameter. The standard deviation was empirically derived in single-individual simulations to reproduce realistic variability in the resulting length, weight, and reproductive rates. This standard deviation reflects the assumed proportion of trait variability due to genetic (heritable) differences:

$$\text{zoom}_i = \mathcal{N}(1, 0.066) \tag{9}$$

$$E_{H,i}^p = E_H^p \cdot \text{zoom}_i \tag{10}$$

$$\{\dot{p}_{Am,i}\} = \{\dot{p}_{Am}\} \cdot \text{zoom}_i \tag{11}$$

$$\{\dot{p}_{Xm,i}\} = \frac{\{\dot{p}_{Am}\}}{\kappa_X} \tag{12}$$

$$[\dot{p}_{M,i}] = \mathcal{N}([\dot{p}_M], \ \sigma), \quad \text{with } \sigma = \text{sardine: } 15; \text{ anchovy: } 5 \tag{13}$$

  - **Without Zoom Factor:** all three parameters are sampled independently from normal distributions centered on their original DEB standard parameter. As above,

standard deviations were empirically tested to be realistic and can be scaled to reflect the fraction of observed variability attributable to genetic differences:

$$E^p_{H,i} = \mathcal{N}(E^p_H, \ \sigma) \quad \text{with } \sigma = \text{sardine: 500; anchovy: 30} \tag{14}$$

$$\{\dot{p}_{Am,i}\} = \mathcal{N}(\{\dot{p}_{Am}\}, \ \sigma) \quad \text{with } \sigma = \text{sardine: 15; anchovy: 0.5} \tag{15}$$

$$\{\dot{p}_{Xm,i}\} = \frac{\{\dot{p}_{Am,i}\}}{\kappa_X} \tag{16}$$

$$[\dot{p}_{M,i}] = \mathcal{N}(p_M, \ \sigma) \quad \text{with } \sigma = \text{sardine: 15; anchovy: 2} \tag{17}$$

Once individual parameters are assigned, the following DEB quantities are computed using standard formulae:

$$L_m = \frac{\kappa \{\dot{p}_{Am,i}\} s_M}{[\dot{p}_M]}, \quad E_m = \frac{\{\dot{p}_{Am,i}\}}{\dot{v}}, \quad g = \frac{[E_G]}{\kappa [E_m]}, \quad k_M = \frac{[\dot{p}_M]}{[E_G]}$$

If not specified, the individual's physical length L_w is sampled from a normal distribution centered on life-stage-appropriate values. Structural length is then calculated as:

$$L = L_w \cdot \delta_M \tag{18}$$

where δ_M is the shape coefficient for converting from physical to structural length and vice-versa. Age is estimated from the ratio of current structural length L to L_m and Age at L_m.

The number of individuals represented by the superindividual (Nind) is set either to a fixed default value (10^7) or passed explicitly by the user. The initial number of individuals at initialization (Nind0) is then back-calculated using cumulative mortality probabilities for each age class (0+ to 4+).

The reproductive buffer E_R is initialized to zero unless otherwise specified. Reserve energy is calculated as:

$$E = f \cdot [E_m] \cdot L^3 \quad \text{and scaled reserve:} \quad e = \frac{E}{[E_m] \cdot L^3}$$

Wet weight is computed as the sum of structure, reserve, and reproduction buffer, if adults (Nisbet et al., 2012):

$$W_w = w \cdot \left(d_V \cdot L^3 + \frac{w_E}{\mu_E}(E + E_R) \right) \tag{19}$$

with w the wet-to-dry conversion factor, d_V the dry density of structure.

Finally, physiological indices such as the condition index (CI), gonadosomatic index (GSI), and dry GSI are computed to assess reproductive condition and energy allocation. The dry

GSI, calculated as the ratio between the dry weight of the gonads and the total body weight, prevents its overestimation by accounting for the fact that eggs hydrate only after being released into the environment.

3.2 Input Data

3.2.1 Environmental Variables

Daily temperature (`Temp`, °C), food availability, expressed as total zooplankton in the basin (`Xtot`, J), along with the day of year at which the simulation should start, are required.

3.2.2 Mortality Rates

Daily age-specific natural mortality (M_0 to M_4) and fishing mortality (MF_0 to MF_4) should be provided. In SPelAgent, both are derived from stock assessments.

3.2.3 DEB Parameters

Parameters for the `abj` DEB model are supplied for sardines and anchovies. Since reproduction rates in the SPelAgent IBM were not satisfactory, sardines were re-parametrized using the Add-my-Pet (AmP) estimation procedure (AmPtool 2024; Marques et al. 2018) available in the DEBtool Matlab package (DEBtool 2024; deblab website) with supplementary data for the Adriatic Sea (Dulčić, 1995; Mustać et al., 2020; Basilone et al., 2023); anchovy parametrization was taken from the AmP collection (Pecquerie and Kooijman 2015; *Engralis encransicolus* - AmP). Parameters of the SPelAgent model are shown in Table 4.

Table 4: Estimated DEB parameters and mortality rates for sardine and anchovy used in SPelAgent

Symbol	Sardine	Anchovy	Unit of measure	Definition
M_{egg}	0.9998	0.9998	-	Egg mortality fraction at hatching
M_0	1.08	1.06	per day	Mortality rate (age 0)
M_1	0.86	1.01	per day	Mortality rate (age 1)
M_2	0.69	0.82	per day	Mortality rate (age 2)
M_3	0.62	0.69	per day	Mortality rate (age 3)
M_4	0.48	0.62	per day	Mortality rate (age 4)
M_{F0}	-	-	per day	Fishing mortality (age 0)
M_{F1}	-	-	per day	Fishing mortality (age 1)
M_{F2}	-	-	per day	Fishing mortality (age 2)
M_{F3}	-	-	per day	Fishing mortality (age 3)
M_{F4}	-	-	per day	Fishing mortality (age 4)
f_{comm}	-	-	-	Communal functional response
$Temp$	-	-	C	Daily temperature from time-series, then converted in Kelvin
T_A	8000.0	9800	K	Arrhenius species specific temperature
T_r	293.0	293.0	K	Reference temperature at which params are calculated
Tc	-	-	-	Temperature correction factor, daily value calculated from the Arrhenius equation
death_thres	-	-	-	Death threshold: fraction to be multiplied by Nind0, below which the SI is removed from the simulation
repro_start	270.0	90.0	day of year	Start of reproduction period
repro_end	90.0	270.0	day of year	End of reproduction period
f_r	400	450	eggsbatch^{-1}g^{-1}	Eggs per gram of free gonad female weight (batch)
κ	0.883	0.9901	-	Allocation fraction to soma
$\dot{p}_{Am}$	554.351	11.1372	J/cm^3/day	Max assimilation coefficient
$\dot{v}$	0.02165	0.01944	cm/day	Energy conductance rate
κ_X	0.8	0.8	-	Digestion efficiency
κ_R	0.95	0.95	-	Reproduction efficiency
$\{\dot{F}_m\}$	6.5	6.5	cm^2/day	Max specific searching rate
δ_M	0.1152	0.1656	-	Shape coefficient

Symbol	Sardine	Anchovy	Unit	Definition
$\dot{k}_J$	0.002	0.002	day^{-1}	Maturity maintenance rate
s_M	2.25531	17.3829	-	Acceleration factor
$\dot{p}_M$	438.602	54.67	J/cm^3/day	Somatic maintenance per unit volume
$[E_g]$	5017.55	5077.00	J/cm^3	Cost per unit of structure
d_V	0.2	0.2	g/cm^3	Specific density of structure (dry)
μ_V	500000.0	500000.0	J/mol	Chemical potential of structure
μ_E	550000.0	550000.0	J/mol	Chemical potential of reserve
w_V	23.9	23.9	g/mol	Molecular dry weight of structure
w_E	23.9	23.9	g/mol	Molecular dry weight of reserve
w	5.0	5.0	J/g	Conversion factor from dry to wet weight
E_H^b	0.01578	0.00012	J	Maturity at birth
E_H^j	0.18735	0.6741	J	Maturity at end of metamorphosis
E_H^p	4553.63	244.0	J	Maturity at puberty
L_b	0.02794	0.01335	-	Structural length at birth
L_j	0.06301	0.23201	-	Structural length at juvenile stage
L_p	1.19937	1.50	-	Structural length at puberty
L_m	2.23	3.47	-	Structural maximum length $Lm = \kappa \dot{p}_{Am} s_M / [\dot{p}_M]$
A_b	6.0	6.0	days	Predicted age at birth from DEB parametrization
A_p	202	292.0	days	Predicted age at puberty from DEB parametrization
A_m	3461	1825.0	days	Predicted lifespan
E_0	0.69402	0.01375	J	Initial reserve $= E_{0max}$
ep_{min}	0.22	0.30	-	scaled reserve density whereby maturation and growth cease at puberty = minimum scaled reserve density of a fertile mother
E_{0min}	0.3	0.004	J	Initial reserve of eggs produced by a fertile mother with scaled reserve density equal to ep_{min}

Symbol	Sardine	Anchovy	Unit	Definition
E_{0max}	0.69402	0.01375	J	Initial reserve of eggs produced by a fertile mother with reserve density equal to $[E_m] = \dot{p}_{Am} / \dot{v}$

3.3 Submodels

3.3.1 Mortality (`die!()`)

Adult mortality is handled by the `adultdie!` function, which incorporates natural, fishing, and thinning-induced mortality. The total mortality rate M is computed as the sum of age-specific daily rate natural mortality M_n, fishing mortality M_f (Hilborn and Walters, 1992), and an optional thinning term h_t (Kooijman, 2024) :

$$M = M_n + M_f + h_t \tag{20}$$

Fishing mortality for age class 0+ is applied to juveniles only if the individual size is larger than 10cm.

Mortality by starvation is described in section 3.3.1.

Thinning Mortality   Thinning extra hazard is a way to counterbalance juveniles' outcompetition of adults due to their relatively high surface-volume ratio (Kooijman 2024; juvenile-driven cycles). Among the artifacts resulting from juvenile-driven cycles, we have high synchronization in reproduction timing of the agents and decreased lifespan of adults due to starvation when juveniles enter the population. In SPelAgent, the thinning hazard formulation is based on the freely available code of the `abj` model in the `popDyn` folder of the `DEB_Tool` repository for DEB parameter estimation (DEBtool, 2024). When the `thinning` option is set to `true` in the `model_initialize!()` function, an additional hazard is applied based on the individual's scaled reserve energy density and structural length to juveniles. If the scaled reserve energy density exceeds the threshold:

$$e \geq \frac{L}{L_m \, s_M}$$

where e is the scaled reserve energy density, L is the structural length, Lm is the maximum structural length, and s_M is the acceleration factor, then the growth rate r is positive and computed as:

$$r = T_c \cdot s_M \cdot v \cdot \frac{e/L - \frac{1}{L_m s_M}}{e + g} \tag{21}$$

where Tc is the temperature correction factor and g is the investment of energy in growth. Otherwise, the growth rate is negative and would imply shrinking of body structure, a phenomenon observed in some species (Kooijman, 2009):

$$r = T_c \cdot s_M \cdot v \cdot \frac{e/L - \frac{1}{L_m s_M}}{e + \kappa_G g} \tag{22}$$

where κ_G is the fraction of growth energy fixed into structure.

The thin hazard h_t is applied only when the growth rate is positive and calculated as:

$$h_t = \frac{2}{3} \frac{r}{c} \tag{23}$$

where $\frac{2}{3}c$ is an adjusted parameter to reduce the effect of hazard and avoid population collapse, while still reducing the effect of juvenile-driven cycles. In fact, around 20% of the species in the AddMyPet database cannot survive thinning (Kooijman, 2024). Other approaches to overcome juvenile-driven cycles would require more complexity, like multiple food resources differentiated according to the life-stage or spatial separation.

The factor c is equal to 5 for sardines and 15 for anchovies, the latter being very high since the anchovies were almost unaffected by the artifacts of juvenile-driven cycles. These values are sufficient to mitigate the effects of juvenile-driven cycles and enable the population to reach a steady state.

Thinning is applied only to juveniles.

Total deaths The number of deaths D is drawn from a binomial distribution:

$$D \sim \text{Binomial}(N_{\text{ind}}, 1 - e^{-M}) \tag{24}$$

If fishing mortality is present, deaths are partitioned between natural and fishing deaths:

$$D_{\text{nat}} \sim \text{Binomial}(D, 1 - e^{-M_n/M}) \tag{25}$$

$$D_{\text{fish}} = D - D_{\text{nat}} \tag{26}$$

The SI size (N_{ind}) is updated by removing the deaths:

$$Nind_{SI\text{t}+1} = Nind_{SI\text{t}} - D \tag{27}$$

If the number of individuals in the SuperIndividual (SI) falls below a threshold, the SI is removed from the simulation:

$$N_{\text{ind}} \leq N_{\text{ind0}} \cdot \text{death\_thres} \tag{28}$$

Here, $N_{\text{ind},0}$ is the initial number of individuals in the SI, and `death_thres` is a scaling factor computed to ensure that, under natural mortality alone, the expected lifespan of the species is respected—10 years for sardines and 7 years for anchovies.

The `death_thres` is calculated at the beginning of the simulation, simulating the decline in Nind inside the SI over time, using age-specific daily mortality rates provided as input. Daily survival is modeled as a binomial process, and the function `calculate_death_thres()` uses binary search to estimate the minimum fraction of the initial number of individuals in the SI (N_{ind0}) that must persist for the population to survive until the maximum lifespan. If the N_{ind} is below this fraction, the SI is removed from the simulation. This provides a biologically consistent and computationally efficient criterion for removing negligible SIs from the simulation.

3.3.2 Energy Dynamics (`DEB!()`)

This submodel updates DEB state variables, calculating at a daily timestep all the energy fluxes described in the section 2.3. Fluxes are influenced by the communal functional response f_{comm} and the current temperature according to the temperature correction factor T_C. Eggs do not assimilate energy from the environment but directly mobilize energy from the reserve. This module also includes the starvation rules (Kooijman, 2009): if the energy mobilized from the reserve is not enough to pay somatic maintenance, juveniles die directly of starvation, while adults are allowed to use the energy stored in the gonads to pay for the deficit. Starvation occurs when mobilized energy cannot cover somatic maintenance:

$$\kappa \cdot \dot{p}_C \leq \dot{p}_S \tag{29}$$

For adults, energy can also be withdrawn from reproductive reserves E_R, and death occurs if the available energy in the reproduction buffer is not enough:

$$E_R \leq \dot{p}_S - \kappa \cdot \dot{p}_C \tag{30}$$

Otherwise, the buffer is used to pay somatic maintenance and is updated as:

$$\Delta E_R = E_R - (\dot{p}_S - \kappa \cdot \dot{p}_C) \tag{31}$$

3.3.3 Hatching (`egghatch!()`)

If $E_H \geq E_H^b$ then the SI become a juvenile and starts to assimilate energy from the environment. A 99.98% of the eggs in the SI are killed at this stage to represent the high early life stage mortality (Haberle et al., 2023).

3.3.4 Maturation (`juvemature!()`)

If $E_H \geq E_H^p$, the SI becomes an adult and starts to store energy in the reproductive buffer.

3.3.5 Aging (`aging!()`)

All the SIs that survive the daily timestep get older by 1 day.

3.3.6 Spawning (`adultspawn!`)

Spawning occurs during a defined reproductive season, from March to September for anchovy and from September to March for sardine (Regner et al., 1987, 1988; Zavodnik, 1969, 1970; Sinovčić and Zorica, 2006). The onset of the reproductive period is subject to inter-individual variability by introducing noise of up to two weeks around the predefined start date:

$$\texttt{reprostart} = \texttt{model.repro\_start} + \mathcal{U}(-14, 14) \tag{32}$$

Spawning is allowed if the current day of the year falls within the species-specific reproductive window. Each individual female produces a number of eggs proportional to its free gonad weight (body weight W_w minus the weight of the reproduction buffer E_R, the latter equal to W_g), scaled by fecundity f_r (eggs batch^{-1} g^{-1}) and perturbed by Gaussian noise to reproduce interindividual variability:

$$N_{\text{eggs}} = (f_r + \mathcal{N}(0, 50)) \cdot (W_w - W_g) \tag{33}$$

The batch fecundity is set at 400 eggs per gram per batch for sardines and 450 eggs per gram per batch for anchovies (Casavola et al., 1996a,b).

The total number of eggs produced by the SI assuming a sex-ratio of 0.5 is:

$$N_{\text{eggs,SI}} = N_{\text{eggs}} \cdot \left\lceil \frac{N_{\text{ind}}}{2} \right\rceil \tag{34}$$

The energy content per egg E_0 is determined according to the maternal effect, i.e., which states that energy density at birth equals the reserve density of the mother at the moment of spawning. The initial energy content of the egg E_0 is then calculated as proposed in Haberle et al. (2023) using the scaled reserve density formulation:

$$E_0 = \left(\frac{E_{0\text{max}} - E_{0\text{min}}}{1 - e_{p\text{min}}} \cdot (e - e_{p\text{min}}) + E_{0\text{min}} \right) + \mathcal{N}(0, 0.1 E_{0\text{min}}) \tag{35}$$

where e is the scaled reserve energy density of the individual, and ep_{min} is the minimal reserve energy density of a fertile mother producing viable eggs. E_{0min} is the energy content of the egg if the scaled reserve energy density of the mother is ep_{min}, and $E_{0\text{max}}$ is the energy content of the egg if the scaled reserve density of the mother is equal to 1, meaning that the reserve density of the mother is equal to $[E_M]$. The total energy to be invested in eggs by a single female is:

$$E_{\text{spawn}} = N_{\text{eggs}} \cdot E_0 \tag{36}$$

Spawning occurs only if this energy is less than or equal to the available energy in the reproductive buffer E_R, scaled by κ_R and subject to a small noise:

$$E_{\text{spawn}} \leq E_R \cdot (\kappa_R + \mathcal{N}(0, 0.01 \kappa_R)) \tag{37}$$

If this condition is met, the sardine is marked as a :spawner, its reproductive buffer is reduced by E_{spawn}, and the spawning counter of the SI is incremented of 1. Otherwise, the individual remains a non-spawner for that time step. Noise added on the start day of reproduction, to individual fertilization, E_0, and to κ_R was introduced to account for inter-individual variability and to avoid artificial thresholds leading to excessive synchronization in reproductive events, increasing the risks of juvenile-driven cycles.

A new SI in the simulation All the eggs produced on the same timestep by the SIs who met the spawning conditions are collected into a new SI, which is added to the simulation with E_0 equal to the mean of the parental E_0, as calculated in Section 3.3.6.

The values of the individual parameters $\{\dot{p}_{Am,i}\}$, $[\dot{p}_{M,i}]$, and $E_{H,i}^p$ are assigned differently depending on whether inheritance is activated once the simulation is initialized. If inheritance is turned off, each new individual receives the standard DEB parameter $\{\dot{p}_{Am}\}$, while $[\dot{p}_M]$ and E_H^p are sampled independently by applying a log-normal variation around the respective reference values (see section 3.1.1).

When inheritance is active, we apply the quantitative genetic principles based on the infinite loci assumption, that is, parameter values are derived from the parental spawner distribution of parameters (Lynch and Walsh, 1998; Robertson and George, 1983; Romero-Mujalli et al., 2019).

When inheritance is active and the zoom factor mechanism is enabled, $\{\dot{p}_{Am}\}$ and E_H^p covary by being multiplied by the same zoom-factor sampled from the parental distribution (Lika et al.

2011; for more details see 3.1.1).

If the zoom mechanism is disabled, we do not assume covariation between $\{\dot{p}_{Am}\}$ and E_H^p values so they will be sampled similarly to $[\dot{p}_{M,i}]$ parental values, with the same standard deviations used at the initialization of the agents (Section 3.1). In this case, the user can decide at initialization whether the normal distributions should be centered on the arithmetic mean or a weighted mean (weighted by the number of eggs spawned by each spawner) of the parental values (section 3.1).

3.4 General Dynamics

3.4.1 Environment Evolution (`evolve_environment!`)

All time-dependent environmental parameters and input time series are updated via the `update_!()` functions, which are called within the `evolve_environment!()` routine.

The parameters updated include:

- **Temperature:** updated from the input daily time series (in °C). Based on temperature, the temperature correction factor T_c is calculated using the Arrhenius equation (see Section 2.3).

- **Food availability:** provided as the total amount of zooplankton energy available in the basin (in Joules).

- **Fishing mortality (F):** age-specific fishing mortality is updated daily, based on annual estimates from stock assessment models for sardine and anchovy.

After updating temperature and food conditions, the communal functional response is calculated following the formulation of Haberle et al. (2023) and assigned to all individuals that feed exogenously (juveniles and adults; see below).

Density dependence. At the individual level, given $\Delta t = 1$ day, we know from section 2.3 that the assimilation flux is:

$$\dot{p}_A = f \cdot \{\dot{p}_{Am}\} \cdot T_c \cdot s_M \cdot L^2 \tag{38}$$

The scaled functional response f can be rewritten as:

$$f = \frac{\dot{p}_A}{\{\dot{p}_{Am}\} \cdot L^2 \cdot T_c \cdot s_M} \tag{39}$$

This formulation can be interpreted as the ratio between the actual assimilation of an individual—given its environment—and the maximum possible assimilation at that temperature and body size.

Following this approach for scaling at the population level, Haberle et al. (2023) introduces the *communal functional response*, f_{comm}, defined as the ratio between the total assimilable food in the water basin ($X_{tot} k_X$), and the theoretical maximum assimilation of the population. This latter is calculated as the sum of the individual maximum theoretical assimilation in the population, accounting for their current size (L^2), the inter-individual variability in $\{\dot{p}_{Am}\}$, and temperature (T_c). Given $\Delta t = 1$ day:

$$f_{\text{comm}} = \frac{X_{\text{tot}} \cdot \kappa_X}{\sum_{i=1}^{N} \dot{p}_{Am,i} \cdot L_i^2 \cdot T_c \cdot s_{Mi} \cdot \Delta t} \tag{40}$$

The numerator represents the actual availability of food in the basin, accounting for assimilation efficiency. The denominator represents the population's theoretical assimilation potential at the given temperature, i.e., the sum over all individuals of their maximum possible assimilation rates, incorporating individual-specific $p_{Am,i}$ values.

This communal response determines the actual functional response f assigned to each feeding individual in the population.

3.4.2 Output Collection

All SuperIndividual (SI) properties (see Table 1) are recorded at each daily time step.

Population-level outputs include aggregated statistics such as:

- Mean structural length, wet weight, and age at puberty

- Total number of individuals alive

- Total biomass by life stage and mortality cause (natural, starvation, fishing)

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