FishErIes Size and functional TYpe model (FEISTY) in R

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Introduction

The R package **FEISTY** is to document the FEITY model and for further model development and research. This document mainly describes the FEISTY model scheme and indicates the corresponding functions in R implementation (Petrik et al. 2019; Denderen et al. 2021).

The structure of main parameters

Several functions to create suitable parameter inputs are included:

- setupBasic creates a basic three-species setup as described in Petrik et al (2019)
- setupBasic2 creates a basic three-species setup as setupBasic(), but generalised to: more realistic sizes, Generalized size-based feeding, the possiblity of more then 3 size groups in each group
- setupVertical makes a basic four-species setup that distinguishes between visual and twilight predators and that includes vertical distribution of zooplankton
- setupPelagicSpecies makes a basic setup with just pelagic fish, and with feeding preferences according to the size ratios of predators and prey.

blabla

Example

The model is first run with the default 3-functional group prameters, created with *setupBasic()*. Then two similar parameter datasets are created, with rates doubled or halved.

```
p <- setupBasic()
knitr::kable(p$resources, digits=2)
```

	K	r	mc	mLower	mUpper	u0
smallZoo	100	1	0.00	NA	NA	NA
largeZoo	100	1	0.02	NA	NA	NA
benthos	5	1	0.25	NA	NA	NA
Spare_position	0	1	5.59	NA	NA	NA

```
knitr::kable(p$fishes, digits=2)
```

	mc	mLower	mUpper	z	psiMature	mortF	mort0	Cmax	metabolism	V
smallPel_1	0.02	0.0	0.5	500	0.0	0.00	0.1	51.72	7.81	149.69
smallPel_2	11.18	0.5	250.0	500	0.5	0.30	0.1	10.94	2.63	43.19
largePel_1	0.02	0.0	0.5	500	0.0	0.00	0.1	51.72	7.81	149.69
largePel_2	11.18	0.5	250.0	500	0.0	0.03	0.1	10.94	2.63	43.19
largePel_3	5590.17	250.0	125000.0	500	0.5	0.30	0.1	2.31	0.89	12.46
demersals_1	0.02	0.0	0.5	500	0.0	0.00	0.1	51.72	7.81	149.69
demersals_2	11.18	0.5	250.0	500	0.0	0.03	0.1	10.94	2.63	43.19
demersals_3	5590.17	250.0	125000.0	500	0.5	0.30	0.1	2.31	0.89	12.46

```
knitr::kable(p$groups, digits=2)
```

	epsRepro	epsAssim
smallPel	0.01	0.7
largePel	0.01	0.7
demersals	0.01	0.7

Function *paramAddPhysiology* is used to change the allometric rates:

```
p2 <- paramAddPhysiology(p, ac = 40, am = 8, ae=140)
```

```
p3 <- paramAddPhysiology(p, ac = 10, am = 2, ae=35)
```

The model can now be run for all parameter sets; the reulst for the last 20 years are shown.

```
out1 <- simulateFEISTY(p=p,  times=seq(0, 200, length.out=1000),bCust=T)
out2 <- simulateFEISTY(p=p2, times=seq(0, 200, length.out=1000),bCust=T)
out3 <- simulateFEISTY(p=p3, times=seq(0, 200, length.out=1000),bCust=T)
# plot(out1, out2, out3, which=5:12, lty=1, lwd=2, subset=time>180)
# plot(out1, out2, out3, which=c("smallZoo", "largeZoo", "smallBenthos",
#   "totBiomass.smallPel", "totBiomass.largePel",  "totBiomass.Demersals"),
#   lty=1, lwd=2, subset=time>180)
```

The FEISTY model

Size spectrum

The fish size span of a functional type is logarithmically discretized into n continuous size bins. Each size bin shares the same ratio z between the upper boundary size and lower boundary size:

$$z = \exp\left(\frac{\ln(w_{max}) - \ln(w_{min})}{n}\right) \tag{1}$$

where w_{min} and w_{max} are smallest and largest fish in a functional type. There are $n + 1$ boundaries of n size bins, including all lower boundary sizes $(m_{l,i})$ and upper boundary sizes $(m_{u,i})$.

$$m_{b,i} = \exp(\ln(w_{min}) + (i - 1)\ln(z)), \qquad i \in [1, n+1] \tag{2}$$

$$m_{l,i} = m_{b,i}, \qquad i \in [1, n] \tag{3}$$

$$m_{u,i} = m_{b,i+1}, \qquad i \in [1, n] \tag{4}$$

The geometric meansize of each size class m_i is:

$$m_i = \exp(\ln(m_{l,i}) + 0.5(\ln(z))), \qquad i \in [1, n] \tag{5}$$

which will be comprehensively used for calculations, for instance, physiological rates and size-based feeding preference.

The size spectrum generation is done by calling the function `paramAddGroup()`. Also, see the source code of `makeGrid()`.

Biomass dynamics

Fish dynamics

The biomass of each size class of a functional type of fish $(B_i,\ gWW\ m^{-2})$ changes over time (t) according to source and sink of energy (De Roos et al. 2008; Petrik et al. 2019):

$$\frac{dB_i}{dt} = J_{in,i} + (\nu_i - \rho_i - \mu_i)B_i - J_{out,i}, \tag{6}$$

where ν_i is the rate of available energy for growth and reproduction, ρ_i is the rate of reproduction, and μ_i $(year^{-1})$ is the total mortality rate. The size of fish increases as a result of growth. The grown fish biomass fluxes out of the current size class to the next size class (excluding the largest fish). The energy fluxing out of a size class i is

$$J_{out,i} = \gamma_i B_i, \tag{7}$$

where γ_i represents the growth rate $(year^{-1})$. The energy fluxing in a size class includes two part for the smallest fish and other sizes, respectively:

$$J_{in,i} = \begin{cases} \epsilon_r \left(J_{out,n} + \sum_i \rho_i B_i \right), & i = 1 \\ J_{out,i-1}, & i > 1 \end{cases} \tag{8}$$

where ϵ_r is the reproduction efficiency. The energy fluxing into the smallest fish class $(i = 1)$ is from the reproduction of each size class of fish that can reproduce and the energy fluxing out of the largest fish class $(J_{out,n})$ because it cannot grow larger. For larger fish $(i > 1)$, the energy fluxing into the size class i is from the growth of the previous neighboring size class $(i - 1)$.

Resource dynamics

The resource i biomass evolves over time according to a chemostat-like growth and a consumption by predators, which is the default resource dynamic mode in four internal setups (Petrik et al. 2019; Denderen et al. 2021):

$$\frac{dR_i}{dt} = r(K_i - R_i) - \mu_{p,i}R_i, \tag{9}$$

where R is the state variable of a resource, K is the carry capacity ($gWW\ m^{-2}$), and r is the growth rate which is constant value (1 $year^{-1}$). μ_p represents the predation mortality on a resource. Alternatively, we provide the logistic growth strategy for resources:

$$\frac{dR_i}{dt} = r_i \cdot R_i \cdot (1 - \frac{R_i}{K_i}) - \mu_{p,i} \cdot R_i, \tag{10}$$

which can be set in `paramAddResource()` function.

Physiological rate

In the FEISTY model, there are three main biological rates based on the allometric scaling relationship of the body size (ref?). The mass-specific maximum consumption rate $C_{max,i}$ ($year^{-1}$), the mass-specific clearance rate V_i ($m^2\ gWW^{-1}\ year^{-1}$), and the mass-specific metabolic rate M_i ($year^{-1}$) for each fish size class are temperature-dependent:

$$C_{max,i} = k_T \cdot a_c \cdot m_i^{b_c} \tag{11}$$

$$V_i = k_T \cdot a_e \cdot m_i^{b_e} \tag{12}$$

$$M_i = k_{TM} \cdot a_m \cdot m_i^{b_m} \tag{13}$$

where k_T and k_{TM} are scaling factors of temperature effects (see Section **Temperature effects**). a_c, a_e, and a_m are intercepts of each biological rate, respectively; b_c, b_e, b_m are exponents. These biological rates determine the energy gained from predation and costs due to basal metabolism (see Section **Energy budget**).

In code implementation, these basic biological rates of fish (without temperature effects) are assigned by the `paramAddPhysiology()` function. The temperature effects on biological rates are added subsequently (see Section **Temperature effects**).

Energy budget

For a given size of fish i, the mass-specific available energy for growth or reproduction (rate) ν_i is the result of the mass-specific energy from assimilated food (rate) minus the mass-specific metabolic rate:

$$\nu_i = \epsilon_\alpha f_i C_{max,i} - M_i \tag{14}$$

where ϵ_α is the assimilation efficiency. The mass-specific feeding level f_i (dimensionless) describes how much food a predator can eat relative to the maximum consumption capability, ranging from 0 to 1:

$$f_i = \frac{E_i}{E_i + C_{max,i}} \tag{15}$$

Therefore, the mass-specific consumption rate $f_i C_{max,i}$ is based on type II functional response. The feeding behavior of a predator is a consequence of encountering prey. The mass-specific encounter rate ($year^{-1}$) E_i of a predator i is:

$$E_i = V_i \sum_j \theta_{i,j} B_j, \tag{16}$$

where $\theta_{i,j}$ denotes the feeding preference of a predator i on a prey j (see Section **?**). B_j represents the biomass of a prey j including zooplankton, benthos or fish. Therefore, the $\sum_j \theta_{i,j} B_j$ represents the biomass of all available prey of a predator.

Reproduction and growth

When the assimilated energy is still surplus after meeting the demand of the basal metabolism, fish can conduct growth and reproduction. The reproductive rate ($year^{-1}$) of each size class of fish is:

$$\rho_i = \begin{cases} \psi_i \nu_i, & \nu_i > 0 \\ 0, & \nu_i \leq 0 \end{cases} \tag{17}$$

ψ_i is the maturity level (dimensionless) of fish i, describing the proportion of available energy (ν_i) used in the reproduction process. It can be either assigned with constants manually (setupBasic and setupVertical (Petrik et al. 2019; Denderen et al. 2021)) or by a sigmoid function (setupBasic2 and setupVertical2):

$$\psi_i = \left(1 + \left(\frac{m_{c,i}}{m_{mature}} \right)^{-5} \right)^{-1} \tag{18}$$

m_{mature} is the half-maturation size of a functional type, which means fish reach 50% maturity level at m_{mature}.

$$m_{mature} = \eta_{mature} w_{max} \tag{19}$$

where η_{mature} is the coefficient determining the half-maturation size relative to the max size of a functional type.

The rest fraction of the available energy ν_i is invested in growth:

$$\kappa_i = 1 - \psi_i \tag{20}$$

The growth rate of a specific size class i is:

$$\gamma_i = \begin{cases} \frac{\kappa_i \nu_i - \mu_i}{1 - (1/z)^{1 - \mu_i / \kappa_i \nu_i}}, & \nu_i > 0 \\ 0, & \nu_i \leq 0 \end{cases} \tag{21}$$

The detail can be found in (De Roos et al. 2008). μ_i is the total mortality including the predation mortality rate ($\mu_{p,i}$), background mortality rate ($\mu_{p,i}$), and fishing mortality rate ($\mu_{f,i}$):

$$\mu_i = \mu_{p,i} + \mu_{b,i} + \mu_{f,i} \tag{22}$$

All size classes of fish a same background mortality rate value within a functional group and the default value is 0.1 $year^{-1}$. The details of predation and fishing are in the sections below.

Predation

In the non-vertical distribution version (setupBasic and setupBasic2) $\theta_{i,j}$ refers to the feeding preference based on the size preference. The value of $\theta_{i,j}$ can be assigned manually (setupBasic, see Table 2 in (Petrik et al. 2019)). It also can be calculated following functions either based on the log-normal distribution:

$$\theta_{i,j} = \begin{cases} \exp \left(-\frac{\left(\log \left(\frac{m_{c,i}}{\beta \cdot m_{c,j}} \right) \right)^2}{(2 \cdot \sigma)^2} \right), & m_i > m_j \\ 0, & m_i \leq m_j \end{cases} \tag{23}$$

or based on the error function (Denderen et al. 2021): ?????????

$$\theta_{i,j} = \frac{\sqrt{\frac{\pi}{2}} \cdot \sigma \cdot \left(\text{erf}\left(\frac{\log(m_{u,j}) - \log\left(\frac{m_{c,i}}{\beta}\right)}{\sqrt{2} \cdot \sigma} \right) - \text{erf}\left(\frac{\log(m_{l,j}) - \log\left(\frac{m_{c,i}}{\beta}\right)}{\sqrt{2} \cdot \sigma} \right) \right)}{\log(m_{u,j}) - \log(m_{l,j})} \tag{24}$$

β is preferred predator-prey mass ratio, and σ is the size preference width for feeding. The size-preference function selection and the values of β and σ can be defined by the function `paramSizepref()`.

In vertical distribution version, $\theta_{i,j}$ is the product of size-based preference ($\theta_{s,i,j}$) and vertical overlap ($\theta_{v,i,j}$):

$$\theta_{i,j} = \theta_{s,i,j} \cdot \theta_{v,i,j} \tag{25}$$

The calculation of $\theta_{s,i,j}$ follows Eq. 23 in setupVertical and Eq. 24 in setupVertical2. The detailed description of $\theta_{v,i,j}$ in the Section **Vertical overlap**.

Once the feeding preference is ready, the predation mortality of a prey j can be calculated:

$$\mu_{p,j} = \sum_i \frac{V_i \theta_{i,j} B_i}{E_i + C_{max,i}} C_{max,i} \tag{26}$$

In practice, the feeding preference setting is more complex, since it plays a vital role in the coexistence of various functional types. when the feeding preference $\theta_{i,j}$ is initially calculated as a function (e.g., Eq. 23), sometimes it needs to be revised or corrected manually according to specific rules, such as cannibalism, habitats, feeding habits, and visibility. Here I introduce how the feeding preference $\theta_{i,j}$ is further processed in setupBasic2.

Forage fish and large pelagic fish live in the pelagic zone during their whole lifetime. Demersal fish habitats are different in terms of their sizes and water depth. Small demersal fish are pelagic status while medium demersal fish are benthic-living. Pelagic-living organisms do not interact with benthic-living organisms and vice versa.

Forage fish
The feeding preference from forage fish and large pelagic fish to benthic resources and medium demersal fish are corrected to 0.

Large pelagic fish
The feeding preference from large pelagic fish to benthic resources and medium demersal fish is corrected to 0. Large pelagic fish have reduced feeding preference on forage fish ($\theta_A \cdot \theta_{i,j}$).

Demersal fish
The feeding preference from small demersal fish to benthic resources is corrected to 0.
Medium demersal fish only feed on benthos and themselves (cannibalism). Therefore, their feeding preference on zooplankton and all fish excluding themselves is corrected to 0.
In shallow water ($< 200m$), large demersal fish swim over the water column, meaning they can eat both pelagic and benthic organisms. Their feeding preference on forage fish was down-regulated: $\theta_A \cdot \theta_D \cdot \theta_{i,j}$. Their feeding preference on large pelagic fish was down-regulated: $\theta_D \cdot \theta_{i,j}$.
When water is deep ($> 200m$), large demersal fish is fully benthic-living. So the feeding preference of large demersals on all pelagic prey is corrected to 0, including forage fish, large pelagic fish, zooplankton, and small demersal fish. They only can feed on benthos, medium demersals, and themselves.

Vertical overlap

To be done...

Fishing

The fishing mortality rate $\mu_{f,i}$ of a particular size class of fish i can be either determined by constant values or by a fishing selectivity function ??????:

$$\mu_{f,i} = \psi_{f,i} F \tag{27}$$

where F is the baseline fishing mortality rate ($year^{-1}$) of a functional type of fish. $\psi_{f,i}$ denotes the size-based fishing selectivity following a sigmoid function:

$$\psi_{f,i} = \left(1 + \left(\frac{m_{c,i}}{m_{fishing}}\right)^{-3}\right)^{-1} \tag{28}$$

where $m_{fishing}$ indicates the fish with this size is under 50% harvesting rate.

$$m_{fishing} = \eta_F w_{max} \tag{29}$$

where η_F controls the weight of fish with 50% harvesting rate relative to the max weight of the functional type. The fishing mortality rate can be assigned by the function `setFishing()`.

Temperature effects

The temperature effects on the mass-specific maximum consumption rate $C_{max,i}$, the mass-specific clearance rate V_i, and the mass-specific metabolic rate M_i (Eq. 11, 12, 13) are based on the use of Q_{10} coefficient, which describes the exponential variation of rates every 10°C.

The general equation for the temperature scaling factor k is:

$$k = Q_{10}^{\frac{T - T_{ref}}{10}} \tag{30}$$

where T_{ref} is the reference temperature and T is the environment temperature. According to the different functional types of fish and their sizes, fish habitats change. For fish staying in the pelagic zone, $T = T_p$ (e.g., all forage fish); for fish always in the benthic zone $T = T_b$ (e.g., medium-size demersal fish). k_T is temperature scaling factor for $C_{max,i}$ and V_i; k_{TM} is temperature scaling factor for M_i. To calculate them, different Q_{10} factors are required (Table xx). The temperature effects on biological rates are done by the function `paramTeffect()`. Note this function only works on non-vertical distribution setups, i.e., setupBasic and setupBasic2. Technically, it also can be used in customized setups.

In setupBasic and setupBasic2, there are three functional types of fish: forage fish (small pelagic fish), large pelagic fish, and demersal fish. Forage fish and large pelagics are always in the pelagic water, so the T_p is consistently applied. Demersal fish habitats change according to size. Small demersal is in a pelagic status (T_p). Medium demersals live at the bottom (T_b). Large demersals also stay in the bottom if the water is deep ($> 200m$). However, in shallow water ($< 200m$), due to their better swimming abilities, the large demersals migrate over the water column for feeding. To better describe the temperature effects on large demersals, the effective temperature is introduced (see Section (**Real-time effective temperature**).

In setupVertical, fish have a new trait axis of vertical distribution.

T profile The implementation is hard-coded, embedded in the function `setupVertical()`

To be done...

To simplify the temperature input, three temperature inputs (T_p, T_m, T_b) are required rather than the water column temperature profile in setupVertical2. Effective temperature of different size classes of each functional type are the averaged values of temperatures of their approximate vertical positions of day (T_{day}) and night (T_{night}).

$$T_e = \frac{T_{day} + T_{night}}{2} \tag{31}$$

Note this T_e is different from the one in the Section **Real-time effective temperature**. The implementation is hard coded in the function `setupVertical2()`.

Small pelagics
They always stay in the pelagic water ($T_{day} = T_{night} = T_p$).

Mesopelagics
At daytime, where mesopelagic fish stay depends on the water column depth and photic conditions:

$$T_{day} = \begin{cases} T_m, & dvm \neq bottom \text{ and } dvm \neq 0 \\ T_b, & dvm = bottom \\ T_p, & dvm = 0 \end{cases} \tag{32}$$

During night time, they are in the pelagic water ($T_{night} = T_p$).

Large pelagics
The large-size classes of large pelagic fish are split into two groups: half of them are always in the pelagic zone, and the habitat of the other half depends on the water column conditions. So their daytime temperature could be the average of two environmental temperatures. If the water column does not support the existence of dvm they all stay in the pelagic zone.

$$T_{day} = \begin{cases} \frac{T_m+T_p}{2}, & dvm \neq bottom \text{ and } dvm \neq 0 \\ \frac{T_b+T_p}{2}, & dvm = bottom \\ T_p, & dvm = 0 \end{cases} \tag{33}$$

All the large pelagics in non-large sizes (small and medium) are in pelagic water the during daytime ($T_{day} = T_p$).
During night time, all of them regardless of size are in the pelagic water ($T_{night} = T_p$).

Bathypelagics
Bathypelagic fish stay at the dvm depth, bottom or pelagic zone, depending on the water column depth and photic conditions at daytime:

$$T_{day} = \begin{cases} T_m, & dvm \neq bottom \text{ and } dvm \neq 0 \\ T_b, & dvm = bottom \\ T_p, & dvm = 0 \end{cases} \tag{34}$$

At night, small and medium bathypelagics are in the pelagic water ($T_{night} = T_p$), but the habitats of large bathypelagics varies with water column conditions:

$$T_{night} = \begin{cases} T_m, & dvm \neq bottom \text{ and } dvm \neq 0 \\ T_b, & dvm = bottom \\ T_p, & dvm = 0 \end{cases} \tag{35}$$

Demersals
Small demersals are pelagic-living ($T_{day} = T_{night} = T_p$); medium demersals are benthic-living ($T_{day} = T_{night} = T_b$). Large demersal fish habitats varies according to the water column conditions.

$$T_{day} = \begin{cases} T_m, & (bottom - dvm) < 1500 \text{ and } bottom \geq photic \\ T_b, & (bottom - dvm) \geq 1500 \\ \frac{T_b+T_p}{2}, & bottom < photic \end{cases} \tag{36}$$

$$T_{night} = \begin{cases} T_b, & bottom \geq photic \\ \frac{T_b+T_p}{2}, & bottom < photic \end{cases} \tag{37}$$

Real-time effective temperature

Following (Petrik et al. 2019), in shallow water ($<200m$) the large demersal fish ($m_{c,i} > 250$ gWW as default) migrate vertically within a day rather than staying at the bottom constantly. They are assumed to spend a fraction of time λ in the pelagic zone and the rest of time $1 - \lambda$ at the bottom according to the abundance of prey in these two zones.

$$\lambda = \frac{B_{pelprey}}{B_{allprey}} \tag{38}$$

where $B_{pelprey}$ denotes the total biomass of pelagic prey for large demersal fish, $B_{allprey}$ is the total biomass of all prey for large demersal fish. A simple case can be found in Eq. 15 in (Petrik et al. 2019).

Therefore, the temperature for large demersals is defined based on their time spent in the pelagic zone and benthic zone, which is called effective temperature:

$$T_e = T_p \cdot \lambda + T_b \cdot (1 - \lambda) \tag{39}$$

T_e is updated each time step during the time integration, along with the temperature-dependent biological rates, which are handled by the function `updateET()`. In code implementation, `updateET()` is called every time step in `derivativesFEISTYR()`. The effective temperature scheme is forced turned on in `setupBasic()` (Petrik et al. 2019); it is an option in `setupBasic2()`.

Default parameters

References

De Roos, André M, Tim Schellekens, Tobias Van Kooten, Karen Van De Wolfshaar, David Claessen, and Lennart Persson. 2008. "Simplifying a Physiologically Structured Population Model to a Stage-Structured Biomass Model." *Theoretical Population Biology* 73 (1): 47–62.

Denderen, P Daniël van, Colleen M Petrik, Charles A Stock, and Ken H Andersen. 2021. "Emergent Global Biogeography of Marine Fish Food Webs." *Global Ecology and Biogeography* 30 (9): 1822–34.

Petrik, Colleen M, Charles A Stock, Ken H Andersen, P Daniël van Denderen, and James R Watson. 2019. "Bottom-up Drivers of Global Patterns of Demersal, Forage, and Pelagic Fishes." *Progress in Oceanography* 176: 102124.

Table 4: Main parameters of FEISTY

Symbol	Description	B1	B2	V1	V2	Unit
a_c	Intercept for mass-specific maximum consumption rate		20			$g^{-b_c}yr^{-1}$
b_c	Exponent for mass-specific maximum consumption rate		-0.25			/
a_e	Intercept for mass-specific clearance rate		70			$m^2g^{-b_e-1}yr^{-1}$
b_e	Exponent for mass-specific clearance rate		-0.2			/
a_m	Intercept for mass-specific metabolism rate	4.015		$0.2{*}a_c$		$g^{-b_m}yr^{-1}$
b_m	Exponent for mass-specific metabolism rate		-0.175			/
ϵ_α	Assimilation efficiency		0.7			/
ϵ_r	Reproduction efficiency		0.01			/
μ_b	Background mortality		0.1			yr^{-1}
F	Baseline fishing mortality rate	/[e]		0		yr^{-1}
η_{mature}	half-maturation size coefficient	/[c]		0.25		/
$\eta_{fishing}$	half-harvesting size coefficient	/[d]		0.05		/
θ_A	Large fish preference on forage fish[b]		0.5	/	/	/
θ_D	Large demersal fish preference on pelagic prey		0.75	/	/	/
aaa	xxx	0.1	0.2	0.3	0.4	gWW
T_{ref}	reference temperature		10			°C
Q_{10}	Rate of change for every 10°C increase for clearance rate and maximum consumption		1.88			/
Q_{10m}	Rate of change for every 10°C increase for metabolism	2.35		1.88		/
aaa	xxx	0.1	0.2	0.3	0.4	gWW
β	Preferred predator:prey mass ratio	/		400		/
σ	Width of size preference for feeding	/		1.3		/
aaa	Continental shelf depth	/	/	250		m
aaa	Photic zone depth	/	/	150		m

[a] B1: setupBasic1, B2: setupBasic2, V1: setupVertcal1, V2: setupVertcal2.

[b] In B1, θ_A only poses on medium forage fish (the second size class). In B2, θ_A works on all forage fish.

[e] In B1, Eq. 27 does not apply. $\mu_{f,i}$ are constant values: Small fish 0 yr^{-1}, Medium fish 0.03 yr^{-1}, Large fish 0.3 yr^{-1}.