FishErIes Size and functional TYpe model (FEISTY) in R

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Introduction

This vignette provides a comprehensive description of the mode equations, parameters, and numerical implementation used in the FishErIes Size and functional TYpe (FEISTY) model system (Petrik et al. 2019; Denderen et al. 2021). This text is followed by several examples illustrating how to use the model within R.

The FEISTY model

The FEISTY model framework is designed to be mechanistic, simple and fast, generally applicable globally, and compatible with biogeochemical model principles. It is based on ordinary differential equations and careful accounting of mass balancing. The model structures fish around functional types (aka. functional groups or guilds) based on traits instead of representing specific species. This simplification, together with the mechanistic basis, allows for projections into novel environments, e.g., climate change projections.

The current FEISTY implementation includes four setups that define which fish functional types are present and how they predate upon one another. Two "Basic" setups contain three functional types: small and large pelagic fish species and demersal species (Petrik et al. 2019). Two "Vertical" setups augment the model with two additional functional types, mesopelagic fish and midwater predators, and further automatize the calculation of the interaction between the functional types based on their vertical overlap (Denderen et al. 2021). The Basic and Vertical setups with the suffix "2" modify the published setups with minor parameter and structural changes. All setups are detailed below.

Regardless of the setup type the biomass dynamics follow the same set of equations, which is detailed in the next section. The differences between the setups lie in how the interactions between the types and sizes are determined, which is detailed in the section "Predation".

Biomass dynamics

Fish dynamics

FEISTY is a size-based model where the biomass of each size class of a functional type of fish (B_i, gWW m^{-2}) [1] changes over time (t) according to source and sink of energy determined by consumption, growth, reproduction and mortality (De Roos et al. 2008). The changes in biomass are described by:

$$\frac{\mathrm{d}B_i}{\mathrm{d}t} = J_{\mathrm{in},i} + (\nu_i - \rho_i - \mu_i)B_i - J_{\mathrm{out},i}, \tag{1}$$

where ν_i is the rate of available energy for growth and reproduction, ρ_i is the rate of reproduction, and μ_i is the total mortality rate. Fish growth leads to a flux out of each size class, which enters the next size class.

[1] gWW: gram wet weight. From now on, we use "g" to represent "gWW" for simplicity.

Since the largest size-class of a functional type cannot grow to an even larger size, the flux out of the last size-class is used for reproduction. The biomass flux out of a size class i is:

$$J_{\text{out},i} = \gamma_i B_i, \tag{2}$$

where γ_i is the growth rate (year^{-1}). The growth flux into a size class differs between the smallest size-class of each functional type and the other sizes. These two parts are:

$$J_{\text{in},i} = \begin{cases} \epsilon_r \left(J_{\text{out},n} + \sum_i \rho_i B_i \right), & i = 1 \\ J_{\text{out},i-1}, & i > 1 \end{cases} \tag{3}$$

where ϵ_r is the reproduction efficiency. The flux into the smallest size class ($i = 1$) is from the reproduction of each size class of mature fish plus the biomass flux out of the maximum size class ($i = n$) of a functional type ($J_{\text{out},n}$). For all other size classes ($i > 1$), the growth flux into the size class i is from the growth of the previous neighboring size class ($i - 1$).

Resource dynamics

FEISTY coupling with the biophysical forcing can be accomplished in three ways: fully two-way (online), production-constrained one-way (offline), and with resources as a semi-chemostat (offline). In case of the latter, the resource i biomass dynamics change over time according to a chemostat-like growth and consumption by fish predators. The modelling of resources as a semi-chemostat is the default resource dynamic mode in the four internal setups:

$$\frac{\mathrm{d}R_i}{\mathrm{d}t} = r(K_i - R_i) - \mu_{\text{p},i} R_i, \tag{4}$$

where R is the state variable of a resource, K is the carrying capacity (g m^{-2}), and r is the growth rate which is a constant value (1 year^{-1}). μ_{p} represents the predation mortality on the resource. Lastly, FEISTY has an option to model resource dynamics with the logistic growth equation:

$$\frac{\mathrm{d}R_i}{\mathrm{d}t} = r_i \cdot R_i \cdot \left(1 - \frac{R_i}{K_i}\right) - \mu_{\text{p},i} \cdot R_i, \tag{5}$$

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

Physiological rates

There are three main biological rates based on the allometric scaling relationship of individual body size: the mass-specific maximum consumption rate $C_{\text{max},i}$ (year^{-1}), the mass-specific clearance rate V_i (m^2 g^{-1} year^{-1}), and the mass-specific metabolic rate M_i (year^{-1}):

$$C_{\text{max},i} = k_{\text{T},i} \cdot a_{\text{c}} \cdot m_i^{b_{\text{c}}} \tag{6}$$

$$V_i = k_{\text{T},i} \cdot a_{\text{e}} \cdot m_i^{b_{\text{e}}} \tag{7}$$

$$M_i = k_{\text{TM},i} \cdot a_{\text{m}} \cdot m_i^{b_{\text{m}}} \tag{8}$$

Here $k_{\text{T},i}$ and $k_{\text{TM},i}$ are scaling factors of temperature effects of each size class (see Section **Temperature effects**). a_{c}, a_{e}, and a_{m} are factors for each biological rate; b_{c}, b_{e}, and b_{m} are exponents. These biological rates determine the energy gained from predation and costs due to basal metabolism (see Section **Energy budget**).

In the code implementation, these basic biological rates of fish (set against the reference temperature of 10°C) are assigned by the `paramAddPhysiology()` function. The scaling of biological rates with temperature is added subsequently (see Section **Temperature effects**).

Energy budget

For a given individual size of fish m_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:

$$\nu_i = \epsilon_\alpha f_i C_{\max,i} - M_i \tag{9}$$

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:

$$f_i = \frac{E_i}{E_i + C_{\max,i}} \tag{10}$$

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:

$$E_i = V_i \sum_j \theta_{i,j} B_j, \tag{11}$$

where $\theta_{i,j}$ denotes the feeding preference of a predator i on a prey j (see Section **Predation**). 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 prey available to a predator.

Reproduction and growth

When the assimilated energy is positive after meeting the metabolic demands, energy is available for fish growth and reproduction (when the available energy is negative, there will be a biomass loss through starvation). The reproductive rate (year^{-1}) of each size class of fish is:

$$\rho_i = \begin{cases} \psi_i \nu_i, & \nu_i > 0 \\ 0, & \nu_i \leq 0 \end{cases} \tag{12}$$

ψ_i is the maturity level (dimensionless) of fish i, describing the proportion of available energy (ν_i) used in the reproduction process. The maturity level can either be assigned manually (setupBasic and setupVertical) or by a sigmoid function (setupBasic2 and setupVertical2):

$$\psi_i = \left(1 + \left(\frac{m_{c,i}}{m_{\text{mature}}}\right)^{-5}\right)^{-1} \tag{13}$$

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

$$m_{\text{mature}} = \eta_{\text{mature}} M \tag{14}$$

where η_{mature} is the coefficient determining the half-maturation size relative to the maximum size (boundary size) of a functional type (M).

κ_i represents the fraction of the available energy (ν_i) invested in growth:

$$\kappa_i = 1 - \psi_i \tag{15}$$

The available energy for growth $\kappa_i \nu_i$ gives a flux of biomass out of the size-class i that depends on the ratio z between the smallest and largest size of the size-class and total mortality μ_i (De Roos et al. 2008):

$$\gamma_i = \begin{cases} \frac{\kappa_i \nu_i - \mu_i}{1 - (1/z)^{1 - \mu_i / \kappa_i \nu_i}}, & \nu_i > 0 \\ 0, & \nu_i \leq 0 \end{cases} \tag{16}$$

μ_i includes a predation ($\mu_{\mathrm{p},i}$), background ($\mu_{\mathrm{b},i}$), and fishing mortality rate ($\mu_{\mathrm{f},i}$):

$$\mu_i = \mu_{\mathrm{p},i} + \mu_{\mathrm{b},i} + \mu_{\mathrm{f},i} \tag{17}$$

All size classes of each functional type experience a background mortality. The details of predation and fishing are described in the sections below.

Predation

FEISTY specifies of how each size class (and zooplankton and benthic prey resources) interact via predator-prey interactions in a feeding preference matrix (also known as a food-web matrix). In this matrix, each element $\theta_{i,j}$ is a number between 0 and 1, which denotes how much a fish class i preys on a prey class j. The feeding preference function is either based on size preference (see Section **Size preference**) or derived from size preference coupling with the vertical habitat of each functional group (see Section **Vertical overlap**). For some combinations of predator and prey, additional modifications are included to account for feeding specializations (see Section **Modifications to the preference matrix**).

Once the preference matrix is established, the predation mortality of a prey j can be calculated:

$$\mu_{\mathrm{p},j} = \sum_i \frac{V_i \theta_{i,j} B_i}{E_i + C_{\mathrm{max},i}} C_{\mathrm{max},i} \tag{18}$$

Size preference

In the non-vertical setups (setupBasic and setupBasic2) $\theta_{i,j}$ refers to the feeding preference based on the size preference. In setupVertical and setupVertical2, it is named $\theta_{s,i,j}$ for differentiation purposes. The value of $\theta_{i,j}$ can be assigned manually (setupBasic, see Table 2 in (Petrik et al. 2019)) or it can be calculated using size-preference functions that are either based on the log-normal distribution (setupBasic2 and setupVertical2):

$$\theta_{i,j} = \begin{cases} \exp\left(-\frac{\left(\log\left(\frac{m_{\mathrm{c},i}}{\beta \cdot m_{\mathrm{c},j}}\right)\right)^2}{(2\cdot\sigma)^2}\right), & m_i > m_j \\ 0, & m_i \leq m_j \end{cases} \tag{19}$$

or the error function (setupVertical, Denderen et al. 2021):

$$\theta_{i,j} = \frac{\sqrt{\frac{\pi}{2}} \cdot \sigma \cdot \left(\mathrm{erf}\left(\frac{\log(m_{\mathrm{u},j}) - \log\left(\frac{m_{\mathrm{c},i}}{\beta}\right)}{\sqrt{2}\cdot\sigma}\right) - \mathrm{erf}\left(\frac{\log(m_{\mathrm{l},j}) - \log\left(\frac{m_{\mathrm{c},i}}{\beta}\right)}{\sqrt{2}\cdot\sigma}\right)\right)}{\log(m_{\mathrm{u},j}) - \log(m_{\mathrm{l},j})} \tag{20}$$

where 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()`.

Vertical overlap

The vertical distribution in setupVertical and setupVertical2 is modeled in a discretized water column:

$$z_\zeta = 0 + \zeta, \qquad \zeta \in [0, z_\mathrm{b}] \tag{21}$$

where ζ is each depth of a water column (integer value), ranging from 0 (surface) to z_{bottom} (sea floor).

The vertical distribution of each size class and functional type i is described as a unimodal distribution:

$$\theta_{\zeta,\mathrm{x},i} = \frac{1}{\sqrt{2\pi\omega_i^2}} \cdot \exp\left(-\frac{(z_\zeta - z_{\mathrm{loc},\mathrm{x},i})^2}{2\omega_i^2}\right) \tag{22}$$

where ω_i gives the vertical range of the vertical distribution of each size class and functional type, x is either day or night, and $z_{\mathrm{loc},\mathrm{x},i}$ is the defined water column depth with the maximum biomass concentration. Some size classes in some functional types have two depths with the maximum biomass concentration $z_{\mathrm{loc},\mathrm{x},i}$. Consequently, they need to be calculated twice and the vertical distribution is the averaged value, which shows a bimodal shape of the vertical distribution. The final vertical distribution in either day or night at each depth of the water column ζ is re-scaled so that the sum over the water column is equal to one:

$$\theta_{\zeta,\mathrm{x},i} = \frac{\theta_{\zeta,\mathrm{x},i}}{\sum\limits_{\zeta} \theta_{\zeta,\mathrm{x},i}} \tag{23}$$

The vertical range of the vertical distribution of each organism ω_i increases with body mass as larger individuals typically have a wider habitat range:

$$\omega_i = \omega_0 + \tau \cdot \log_{10}\left(\frac{m_{\mathrm{c},i}}{m_{\mathrm{c},0}}\right) \tag{24}$$

where ω_0 is the baseline range of the vertical distribution and τ is the range-increasing factor of vertical distribution. $m_{\mathrm{c},0}$ denotes the reference size to which all organisms are scaled in the simulation (typically small mesozooplankton).

Vertical overlap between predator and prey is then estimated as the lowest value between vertical distribution values of a specific predator i and a prey j at depth ζ at daytime or nighttime x $\min(\theta_{\zeta,\mathrm{x},i}, \theta_{\zeta,\mathrm{x},j})$. The depth-integration gives the synthetic vertical overlap value of predator i to a prey j at day or night $\theta_{\mathrm{v},\mathrm{x},i,j}$:

$$\theta_{\mathrm{v},\mathrm{x},i,j} = \sum_{\zeta} \min(\theta_{\zeta,\mathrm{x},i}, \theta_{\zeta,\mathrm{x},j}) \tag{25}$$

Ultimately, the total vertical overlap is the averaged value of the synthetic day and night vertical overlap values:

$$\theta_{\mathrm{v},i,j} = \frac{\theta_{\mathrm{v},\mathrm{day},i,j} + \theta_{\mathrm{v},\mathrm{night},i,j}}{2} \tag{26}$$

This depth integrated vertical overlap value $\theta_{\mathrm{v},i,j}$ is combined with the size-based preference $\theta_{\mathrm{s},i,j}$ and used for the calculation of feeding preference $\theta_{i,j}$:

$$\theta_{i,j} = \theta_{\mathrm{s},i,j} \cdot \theta_{\mathrm{v},i,j} \tag{27}$$

Vertical habitats of resources and fish

Regardless of water conditions, Benthos are concentrated at the bottom ($z_{\mathrm{loc},\mathrm{day},i} = z_{\mathrm{loc},\mathrm{night},i} = z_{\mathrm{bottom}}$) and to ensure they remain closely associated with the sea floor, their vertical range is kept as the baseline value $\omega_i = \omega_0$ (used in Eq. 22).

The vertical habitat strategy of fish depends on seafloor depth and varies between fish functional types. Small and large pelagics and demersal fish make up the fish community in shelf regions, i.e. regions < 250 meters in depth. In these regions, zooplankton prey, small and large pelagics are distributed in the upper water column with a maximum concentration at the surface of the water column ($z_{\mathrm{loc},\mathrm{day},i} = z_{\mathrm{loc},\mathrm{night},i} = 0$). Demersal fish change their vertical distribution throughout ontogeny [2]: small-size classes feed in the upper water column ($z_{\mathrm{loc,day},i} = z_{\mathrm{loc,night},i} = 0$), medium-size classes feed at the bottom ($z_{\mathrm{loc,day},i} = z_{\mathrm{loc,night},i} = z_{\mathrm{bottom}}$), and large-size classes, if the water column is full of light ($z_{\mathrm{bottom}} \leq z_{\mathrm{photic}}$), exhibit cross-habitat feeding between the bottom and the surface waters all the day with maximum concentrations at the surface and the bottom (two $z_{\mathrm{loc,x},i}$ for each day and night: 0 and z_{bottom}). If ($z_{\mathrm{bottom}} > z_{\mathrm{photic}}$) large demersal fish stay at surface waters during daytime ($z_{\mathrm{loc,day},i} = 0$) and bottom at night ($z_{\mathrm{loc,night},i} = z_{\mathrm{bottom}}$).

In slope and open ocean regions, some zooplankton resources and size classes of specific fish functional types conduct diel vertical migration to the depth z_{dvm} (z_{dvmdem} for large demersal fish, described later), which is the representative depth of maximum biomass concentration:

$$z_{\mathrm{dvm}} = \begin{cases} z_{\mathrm{photc}} + 500, & z_{\mathrm{bottom}} \geq z_{\mathrm{photic}} + 500 \\ z_{\mathrm{bottom}}, & z_{\mathrm{photic}} + 500 > z_{\mathrm{bottom}} > z_{\mathrm{shelf}} \\ 0, & z_{\mathrm{bottom}} \leq z_{\mathrm{shelf}} \end{cases} \tag{28}$$

The migrating part of the zooplankton community is at depth during the day and at the surface at night, whereas the remaining zooplankton stay at the surface waters the whole day ($z_{\mathrm{loc,day},i} = 0$ *and* z_{dvm}; $z_{\mathrm{loc,night},i} = 0$). As a result, during the day, zooplankton have a bimodal distribution with maximum concentration depths at the surface and in the twilight zone.
Small pelagics are distributed in the upper water column with a maximum concentration at the surface water ($z_{\mathrm{loc,day},i} = z_{\mathrm{loc,night},i} = 0$).
Mesopelagic fish follow the day/night vertical movement of the migrating zooplankton with a maximum concentration at similar depths ($z_{\mathrm{loc,day},i} = z_{\mathrm{dvm}}$; $z_{\mathrm{loc,night},i} = 0$).
Large pelagics, perform differently throughout ontogeny. The small- and medium-size classes are distributed in the upper water column with a maximum concentration at the surface at day and night ($z_{\mathrm{loc,day},i} = z_{\mathrm{loc,night},i} = 0$). The large size-classes have a bimodal distribution during the day, where half are distributed in the upper water column with a maximum concentration at the surface ($z_{\mathrm{loc,day},i} = 0$), and the other half have a maximum concentration in the midwater ($z_{\mathrm{loc,night},i} = z_{\mathrm{dvm}}$). At night, they are distributed in the upper water column ($z_{\mathrm{loc,night},i} = 0$).
Small- and medium-size classes of midwater predators have the same vertical distribution as mesopelagic fish ($z_{\mathrm{loc,day},i} = z_{\mathrm{dvm}}$; $z_{\mathrm{loc,night},i} = 0$). Large midwater predators have a maximum concentration in midwater ($z_{\mathrm{loc,day},i} = z_{\mathrm{loc,night},i} = z_{\mathrm{dvm}}$).
Small demersals are distributed in the upper water column with a maximum concentration at the surface both day and night ($z_{\mathrm{loc,day},i} = z_{\mathrm{loc,night},i} = 0$). Medium demersal fish are distributed near the bottom ($z_{\mathrm{loc,day},i} = z_{\mathrm{loc,night},i} = z_{\mathrm{bottom}}$). Large demersal fish have a vertical habitat strategy that differs from the other groups. At night, large demersal fish are at the bottom ($z_{\mathrm{loc,night},i} = z_{\mathrm{bottom}}$), while during the day, the depth of maximum concentration z_{dvmdem} is:

$$z_{\mathrm{dvmdem}} = \begin{cases} z_{\mathrm{dvm}}, & z_{\mathrm{bottom}} - z_{\mathrm{dvm}} < 1200 \\ z_{\mathrm{bottom}} - 1200, & 1200 \leq z_{\mathrm{bottom}} - z_{\mathrm{dvm}} < 1500 \\ z_{\mathrm{bottom}}, & z_{\mathrm{bottom}} - z_{\mathrm{dvm}} \geq 1500 \end{cases} \tag{29}$$

Table 1 showed a summary of vertical habitats for different resources and functional types.

[2] small-, medium-, and large-size classes of fish are distinguished by comparison between the geometric mean mass value ($m_{\mathrm{c},i}$) and boundary mass value (m_{medium} or m_{large}). Small-size class: $m_{\mathrm{c},i} < m_{\mathrm{medium}}$. Medium-size class: $m_{\mathrm{medium}} \leq m_{\mathrm{c},i} \leq m_{\mathrm{large}}$. Large-size class: $m_{\mathrm{c},i} > m_{\mathrm{large}}$. Default $m_{\mathrm{medium}} = 0.5$g and $m_{\mathrm{large}} = 250$g .

Table 1: Representative depth of maximum biomass of each size class $z_{\text{loc,x},i}$ at day and night. z_{dvm} and z_{dvmdem} can be found in Eq. 28 and 29.

	Day			Night		
Resources						
Zooplankton[a]	0 and z_{dvm}			0		
Benthos	z_{bottom}			z_{bottom}		
Fish	Small	Medium	Large	Small	Medium	Large
Small pelagic fish	0	0	/	0	0	/
Mesopelagic fish	z_{dvm}	z_{dvm}	/	0	0	/
Large pelagic fish	0	0	0 and z_{dvm}	0	0	0
Midwater predators	z_{dvm}	z_{dvm}	z_{dvm}	0	0	z_{dvm}
Demersal fish	0	z_{bottom}	z_{dvmdem}[b]	0	z_{bottom}	z_{bottom}[b]

[a] Zooplankton include small and large mesozooplankton

[b] If the water column is shallower than the photic zone depth ($z_{\text{bottom}} \leq z_{\text{photic}}$), large demersal fish migrate over the water column (two $z_{\text{loc,x},i}$ for each day and night: z_{dvmdem} and z_{bottom}). In such cases, $z_{\text{dvmdem}} = 0$.

Modifications to the preference matrix

`setupBasic2`

- The feeding preference from small pelagic and large pelagic fish to benthic resources and medium demersal fish are set to 0.
- Large pelagic fish have a reduced feeding preference for medium-sized small pelagic fish ($\theta_{\text{A}} \cdot \theta_{i,j}$).
- The feeding preference from small demersal fish to benthic resources is set 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.
- Large demersal fish eat both pelagic and benthic organisms in shallow water ($<$ 200 m). They are less efficient at attacking pelagic prey and hence their feeding preference on small pelagic fish is down-regulated: $\theta_{\text{A}} \cdot \theta_{\text{D}} \cdot \theta_{i,j}$; similarly for their feeding preference on large pelagic fish: $\theta_{\text{D}} \cdot \theta_{i,j}$. In deeper waters ($>$ 200 m), large demersal fish only feed on benthos, medium demersals, and themselves.

`setupVertical and setupVertical2`

- Small and large pelagics are visual predators whose predation ability is better in light-rich waters during the day and worse in dark conditions such as night or the twilight zone. Therefore, according to habitats (Table 1), the vertical overlap is modified by multiplying it with a visual scaling factor θ_{visual}:

  $$\theta_{\text{v},x,i,j} = \theta_{\text{v},x,i,j} \cdot \theta_{\text{visual}}. \tag{30}$$

  During daytime, the vertical overlap of all small and large pelagics on all preys in surface waters ($\theta_{\text{v},day,i,j}$) is enhanced ($\theta_{\text{visual}} = 1.5$); the vertical overlap ($\theta_{\text{v},day,i,j}$) of large size classes of large pelagics on the preys in the twilight zone (z_{dvm}) (mesopelagic fish and midwater predators) is reduced ($\theta_{\text{visual}} = 0.5$). At night, their vertical overlap on all preys ($\theta_{\text{v},night,i,j}$) is decreased ($\theta_{\text{visual}} = 0.5$). Note this modification is done before Eq. 26.
- The feeding preference from all size-classes that are pelagic-living (small pelagics, mesopelagics, large pelagics, midwater predators and small size classes of demersal fish) to benthic resources are set to 0. In addition, their feeding preference on medium demersal fish (benthic-living) is reduced ($\theta_{i,j} = \theta_{i,j} \cdot 0.25$).
- The feeding preference of medium and large demersal fish to zooplankton resources are set to 0.

- All large-size classes of pelagic-living functional fish groups (large pelagic fish, midwater predators, and demersal fish) have reduced feeding preference on medium-size small pelagic fish and medium-size mesopelagic fish ($\theta_{i,j} = \theta_{i,j} \cdot \theta_{\mathrm{A}}$).

Fishing mortality

The fishing mortality rate $\mu_{\mathrm{f},i}$ of a particular size class of fish i can be either determined by constant values or by a fishing selectivity function (Andersen 2019, chap. 5):

$$\mu_{\mathrm{f},i} = \psi_{\mathrm{f},i} F_{\max} \tag{31}$$

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

$$\psi_{\mathrm{f},i} = \left(1 + \left(\frac{m_{\mathrm{c},i}}{m_{\mathrm{fishing}}}\right)^{-3}\right)^{-1} \tag{32}$$

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

$$m_{\mathrm{fishing}} = \eta_{\mathrm{F}} M \tag{33}$$

where η_{F} controls the weight of fish with a 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. 6, 7, 8) are based on the use of the Q_{10} coefficient, which describes the exponential variation of rates every 10°C.

The general equation for the temperature scaling factor k is:

$$k = Q_{10}^{\frac{T - T_{\mathrm{ref}}}{10}} \tag{34}$$

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, $T = T_{\mathrm{p}}$, which reflects the average temperature in the top 100m of the water column. For fish in the benthic zone, $T = T_{\mathrm{b}}$, which reflects the temperature near the bottom. Through introducing different Q_{10} coefficients (Table 2), various temperature scaling factors k can be obtained. k_{T} is the temperature scaling factor for $C_{\max,i}$, and V_i; k_{TM} is the temperature scaling factor for M_i.

setupBasic and setupBasic2

In `setupBasic` and `setupBasic2`, there are three functional types of fish: small pelagic fish, large pelagic fish, and demersal fish. Small pelagics 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 fish are 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 ($>$ 200 m). However, in shallow water ($<$ 200 m), large demersals 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:

$$\lambda = \frac{B_{\mathrm{pelprey}}}{B_{\mathrm{allprey}}} \tag{35}$$

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:

$$T_{\mathrm{e}} = T_{\mathrm{p}} \cdot \lambda + T_{\mathrm{b}} \cdot (1-\lambda) \tag{36}$$

In code implementation, 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`. T_{e} is updated each time step during the time integration, along with the temperature-dependent biological rates of large demersals, which are handled by the function `updateET()`. The function `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()`.

setupVertical

In setupVertical, fish have a vertical distribution. Temperature effects on physiological rates of each size class are based on where fish stay in a water column (environmental temperature). Therefore the total vertical distribution data needs to be calculated initially:

$$\theta_{\zeta,i} = \frac{\theta_{\zeta,\mathrm{day},i} + \theta_{\zeta,\mathrm{night},i}}{2} \tag{37}$$

Then the temperature scaling factor of each size class in a discretized water column can be obtained according to their vertical distribution:

$$k_{\zeta,i} = \theta_{\zeta,i} \cdot Q_{10}^{\frac{T_\zeta - T_{\mathrm{ref}}}{10}} \tag{38}$$

where the water column temperature profile ranging from the surface (0 m) to the bottom, which can be obtained from observational data products or earth system model outputs. Finally, the scaling factor is integrated over the vertical distribution.

$$k_i = \sum_{\zeta} k_{\zeta,i} \tag{39}$$

k_i can be used in temperature effects on physiological rates Eq. 6, 7, 8. The implementation is hard-coded, and embedded in the function `setupVertical()`.

setupVertical2

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. T_{m} represents the averaged mid-water temperature (500 - up to 1500 m). If T_{m} is not provided, $T_{\mathrm{m}} = T_{\mathrm{b}}$ The 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}).

$$T_{\mathrm{e}} = \frac{T_{\mathrm{day}} + T_{\mathrm{night}}}{2} \tag{40}$$

Note this T_{e} is different from the one in setupBasic and setupBasic2. The T_{e} is taken into Eq. 34 as T, and updates the temperature-dependent physiological rates (Eq. 6, 7, 8). The implementation is hard-coded in the function `setupVertical2()`.

The temperatures associated with each size class and functional type follow the vertical distributions:

- Small pelagics always stay in the surface pelagic waters ($T_{\mathrm{day}} = T_{\mathrm{night}} = T_{\mathrm{p}}$).
- Mesopelagics at night stay in the surface pelagic waters ($T_{\mathrm{night}} = T_{\mathrm{p}}$), whereas their vertical distribution varies with depth and photic conditions during the day:

$$T_{\text{day}} = \begin{cases} T_{\text{m}}, & z_{\text{dvm}} \neq z_{\text{bottom}} \text{ and } z_{\text{dvm}} \neq 0 \\ T_{\text{b}}, & z_{\text{dvm}} = z_{\text{bottom}} \\ T_{\text{p}}, & z_{\text{dvm}} = 0 \end{cases} \tag{41}$$

- The small and medium-sized classes of large pelagics are in the surface pelagic waters both day and night ($T_{\text{day}} = T_{\text{night}} = T_{\text{p}}$). The large-sized classes of large pelagic fish are in the surface pelagic waters at night ($T_{\text{night}} = T_{\text{p}}$) and they are split into two groups during the day: half of them are always in the surface pelagic zone, and the habitat of the other half depends on the water column conditions. Their daytime temperature is the average of these two environmental temperatures:

$$T_{\text{day}} = \begin{cases} \frac{T_{\text{m}}+T_{\text{p}}}{2}, & z_{\text{dvm}} \neq z_{\text{bottom}} \text{ and } z_{\text{dvm}} \neq 0 \\ \frac{T_{\text{b}}+T_{\text{p}}}{2}, & z_{\text{dvm}} = z_{\text{bottom}} \\ T_{\text{p}}, & z_{\text{dvm}} = 0 \end{cases} \tag{42}$$

- Midwater predators at daytime stay at the dvm depth, bottom, or surface pelagic zone, depending on the water column depth and photic conditions:

$$T_{\text{day}} = \begin{cases} T_{\text{m}}, & z_{\text{dvm}} \neq z_{\text{bottom}} \text{ and } z_{\text{dvm}} \neq 0 \\ T_{\text{b}}, & z_{\text{dvm}} = z_{\text{bottom}} \\ T_{\text{p}}, & z_{\text{dvm}} = 0 \end{cases} \tag{43}$$

  At nighttime, small and medium midwater predators are in the surface pelagic waters ($T_{\text{night}} = T_{\text{p}}$), whereas the habitat of large midwater predators varies with water column conditions:

$$T_{\text{night}} = \begin{cases} T_{\text{m}}, & z_{\text{dvm}} \neq z_{\text{bottom}} \text{ and } z_{\text{dvm}} \neq 0 \\ T_{\text{b}}, & z_{\text{dvm}} = z_{\text{bottom}} \\ T_{\text{p}}, & z_{\text{dvm}} = 0 \end{cases} \tag{44}$$

- Small demersals are pelagic-living ($T_{\text{day}} = T_{\text{night}} = T_{\text{p}}$); medium demersals are benthic-living ($T_{\text{day}} = T_{\text{night}} = T_{\text{b}}$). Large demersal fish habitats vary according to the water column conditions.

$$T_{\text{day}} = \begin{cases} T_{\text{m}}, & (z_{\text{bottom}} - z_{\text{dvm}}) < 1500 \text{ and } z_{\text{bottom}} \geq z_{\text{photic}} \\ T_{\text{b}}, & (z_{\text{bottom}} - z_{\text{dvm}}) \geq 1500 \\ \frac{T_{\text{b}}+T_{\text{p}}}{2}, & z_{\text{bottom}} < z_{\text{photic}} \end{cases} \tag{45}$$

$$T_{\text{night}} = \begin{cases} T_{\text{b}}, & z_{\text{bottom}} \geq z_{\text{photic}} \\ \frac{T_{\text{b}}+T_{\text{p}}}{2}, & z_{\text{bottom}} < z_{\text{photic}} \end{cases} \tag{46}$$

Setup of the size spectrum grid

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:

$$z = \exp\left(\frac{\ln(M) - \ln(M_0)}{n}\right) \tag{47}$$

where M_0 and M are the smallest and largest fish in a functional type (boundary size). There are $n+1$ boundaries of n size bins ($m_{\mathrm{b},i}$), including all lower boundary sizes ($m_{\mathrm{l},i}$) and upper boundary sizes ($m_{\mathrm{u},i}$).

$$m_{\mathrm{b},i} = \exp(\ln(M_0) + (i-1)\ln(z)), \qquad i \in [1, n+1] \tag{48}$$

$$m_{\mathrm{l},i} = m_{\mathrm{b},i}, \qquad i \in [1, n] \tag{49}$$

$$m_{\mathrm{u},i} = m_{\mathrm{b},i+1}, \qquad i \in [1, n] \tag{50}$$

The geometric mean size of each size class m_i is:

$$m_i = \exp(\ln(m_{\mathrm{l},i}) + 0.5(\ln(z))), \qquad i \in [1, n] \tag{51}$$

which can 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()`.

Default parameters

Table 2: Main parameters of FEISTY

Symbol	Description	Value[a]				Unit
		B1	B2	V1	V2	
a_{c}	Intercept for mass-specific maximum consumption rate	20				$\mathrm{g}^{-b_{\mathrm{c}}}\mathrm{yr}^{-1}$
b_{c}	Exponent for mass-specific maximum consumption rate	-0.25				/
a_{e}	Intercept for mass-specific clearance rate	70				$\mathrm{m}^2\mathrm{g}^{-b_{\mathrm{e}}-1}\mathrm{yr}^{-1}$
b_{e}	Exponent for mass-specific clearance rate	-0.2				/
a_{m}	Intercept for mass-specific metabolism rate	0.2*a_{c}				$\mathrm{g}^{-b_{\mathrm{m}}}\mathrm{yr}^{-1}$
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}
$F_{\max}$	Maximum fishing mortality rate	0[b]				yr^{-1}
η_{mature}	half-maturation size coefficient	/[c]	0.25			/
η_{fishing}	half-harvesting size coefficient	/[d]	0.05			/
θ_{A}	Large fish preference on small pelagic fish[e]	0.5				/
θ_{D}	Large demersal fish preference on pelagic prey	0.75		/	/	/
ω_0	baseline range of the vertical distribution	/		10		/
τ	range-increasing factor of vertical distribution	/		10		/
T_{ref}	reference temperature	10				°C
Q_{10}	Rate of change for every 10°C increase for clearance rate and maximum consumption	1.88				/
$Q_{10\mathrm{m}}$	Rate of change for every 10°C increase for metabolism	2.35		1.88		/
β	Preferred predator:prey mass ratio	/	400			/
σ	Width of size preference for feeding	/	1.3			/
z_{shelf}	Continental shelf depth	/	/	250		m
z_{photic}	Photic zone depth	/	/	150		m
m_{medium}	boundary size of small/medium fish class	0.5				g
m_{large}	boundary size of medium/large fish class	250				g

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

[b] In B1, the fishing mortality can also be assigned manually [@petrik2019bottom] (Eq. 31 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}.

[c] Maturity level ψ_i is assigned manually in default B1. Only the last stage of each functional type has a value of 0.5 others are 0.

[d] Fishing mortality $\mu_{f,i}$ is 0 in default B1.

[e] In B1, θ_{A} only poses on medium-sized classes of small pelagic fish (the second size class). In B2, θ_{A} works on all small pelagic fish. In V1 and V2, θ_{A} works on medium-sized classes of small pelagic and mesopelagic fish.

Demonstration

FESITY includes four setups which each specifies the available functional groups and their parameters:

- setupBasic creates a basic three-functional type setup as described in (Petrik et al. 2019).
- setupBasic2 creates the same three-functional type setup as setupBasic(), but it allows more size numbers in each functional type, size-based maturity, generalized size-based feeding preference, and size-based fishing mortality.

- setupVertical makes a basic five-functional type setup that includes vertical distribution of resources and fish (Denderen et al. 2021).
- setupVertical2 is the same as setupVertical but different it allows more size numbers in each functional type, size-based maturity, generalized size-based feeding preference, size-based fishing mortality, and simpler temperature input.

Basic simulation and visualization

Here we demonstrate some examples of the basic usage of simulating FEISTY and visualization. Before a FEISTY simulation, first, we need to generate a full parameter set:

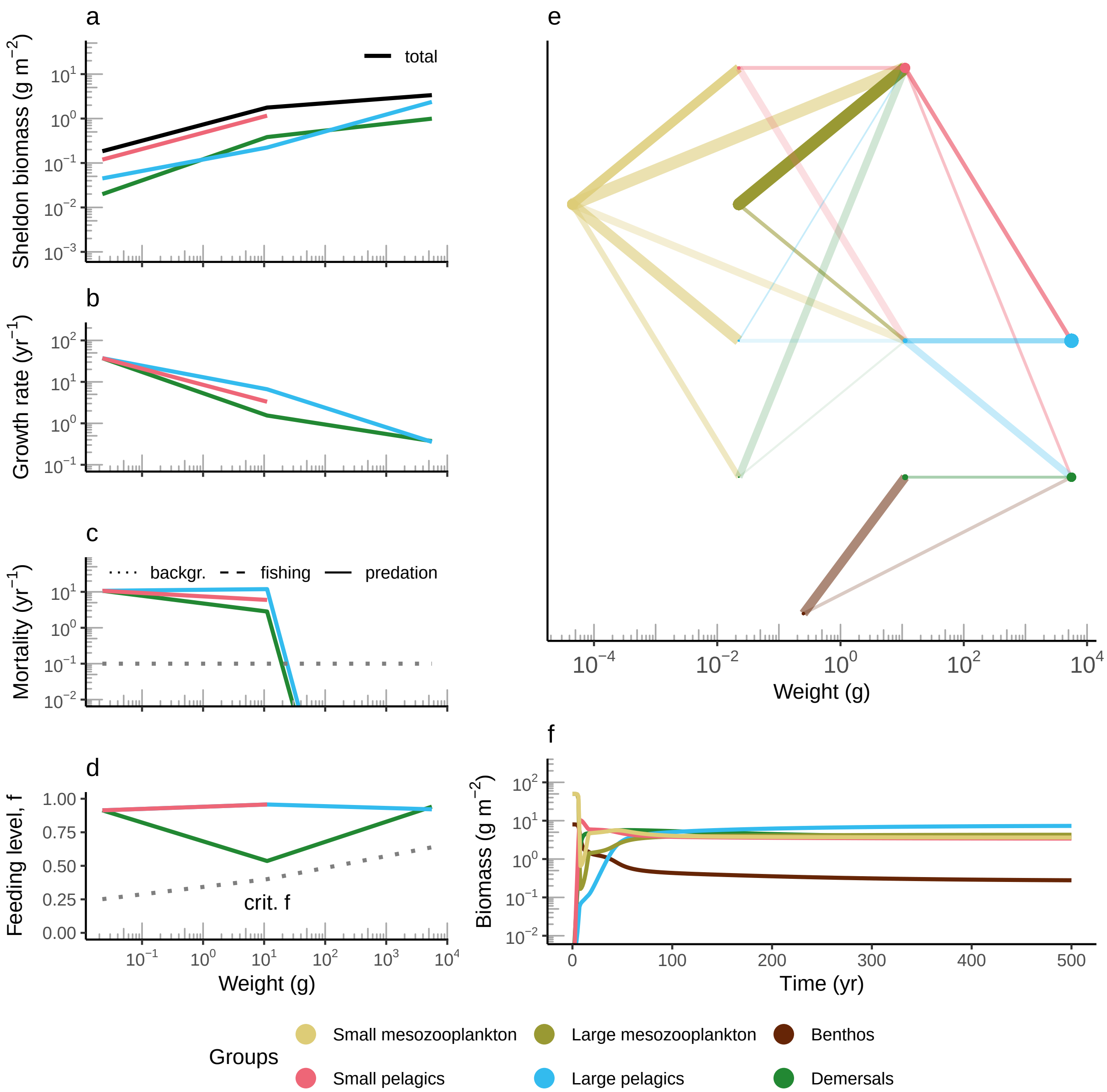
```
p <- setupBasic(szprod = 50,   # small mesozooplankton production
                lzprod = 50,   # large mesozooplankton production
                bprodin  = 8,  # benthos production
                depth  = 150,  # water column depth [m]
                Tp     = 17,   # pelagic layer averaged temperature [Celsius]
                Tb     = 12)   # sea floor temperature [Celsius]
```

This parameter set contains three functional types according to (Petrik et al. 2019), created by `setupBasic()`. Once the parameter set is ready, we can run the simulation by `simulateFEISTY()`:

```
sim <- simulateFEISTY(p=p,  times=seq(0, 500, length.out=500), USEdll = T)
```

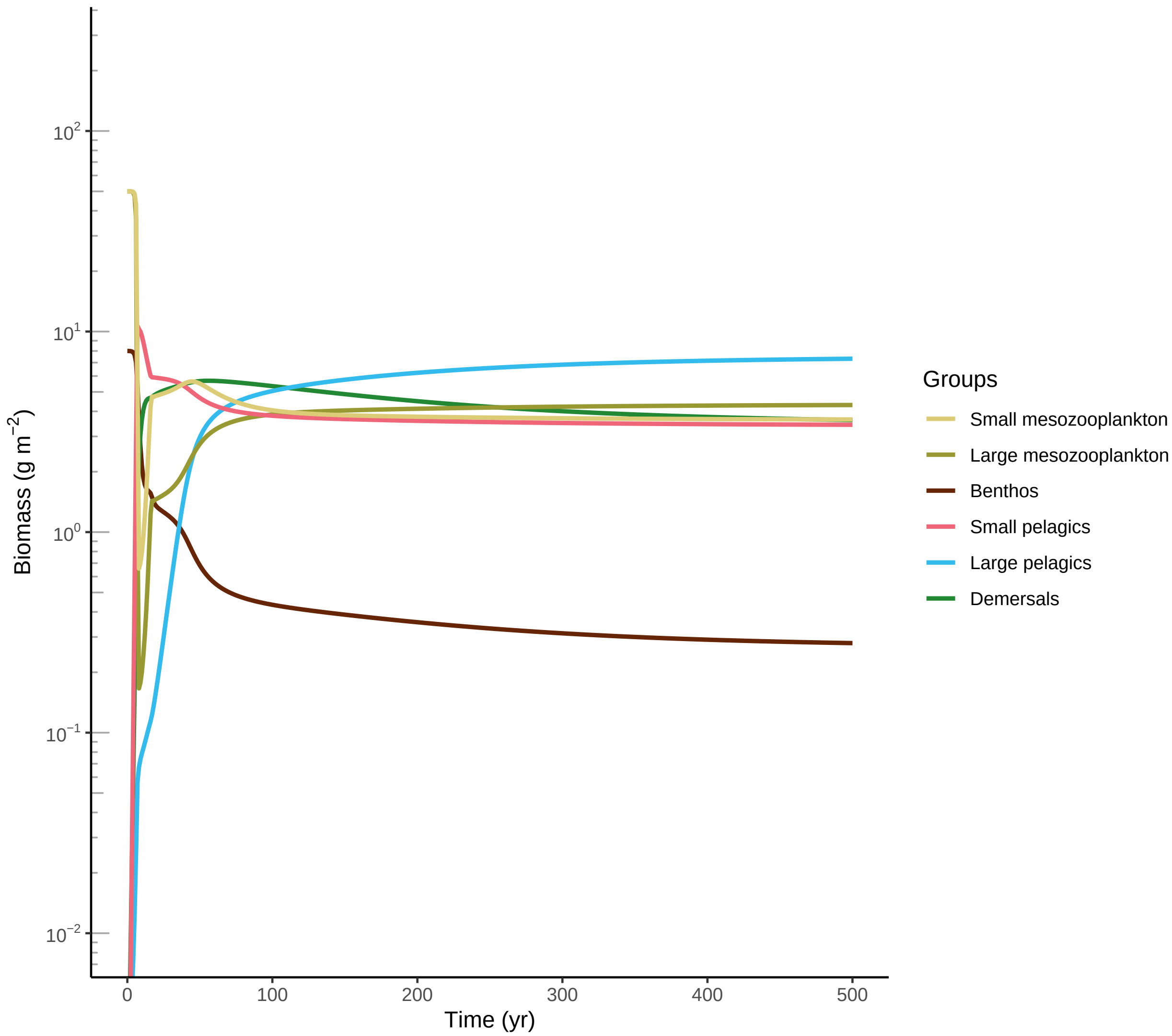
This simulation runs 500 years based on the parameter set `p` we defined above, and the time series output is in every year. `USEdll = T` denotes an almost identical parameter will be generated in the Fortran dll based on the arguments provided in `setupBasic()` and the core computation will be done by the Fortran dll and ultimately the results will be returned to R. Then we can visualize the simulation result. To get an overview, we can use `plotSimulation()` which gives information though a figure collection:

```
plotSimulation(sim)
```

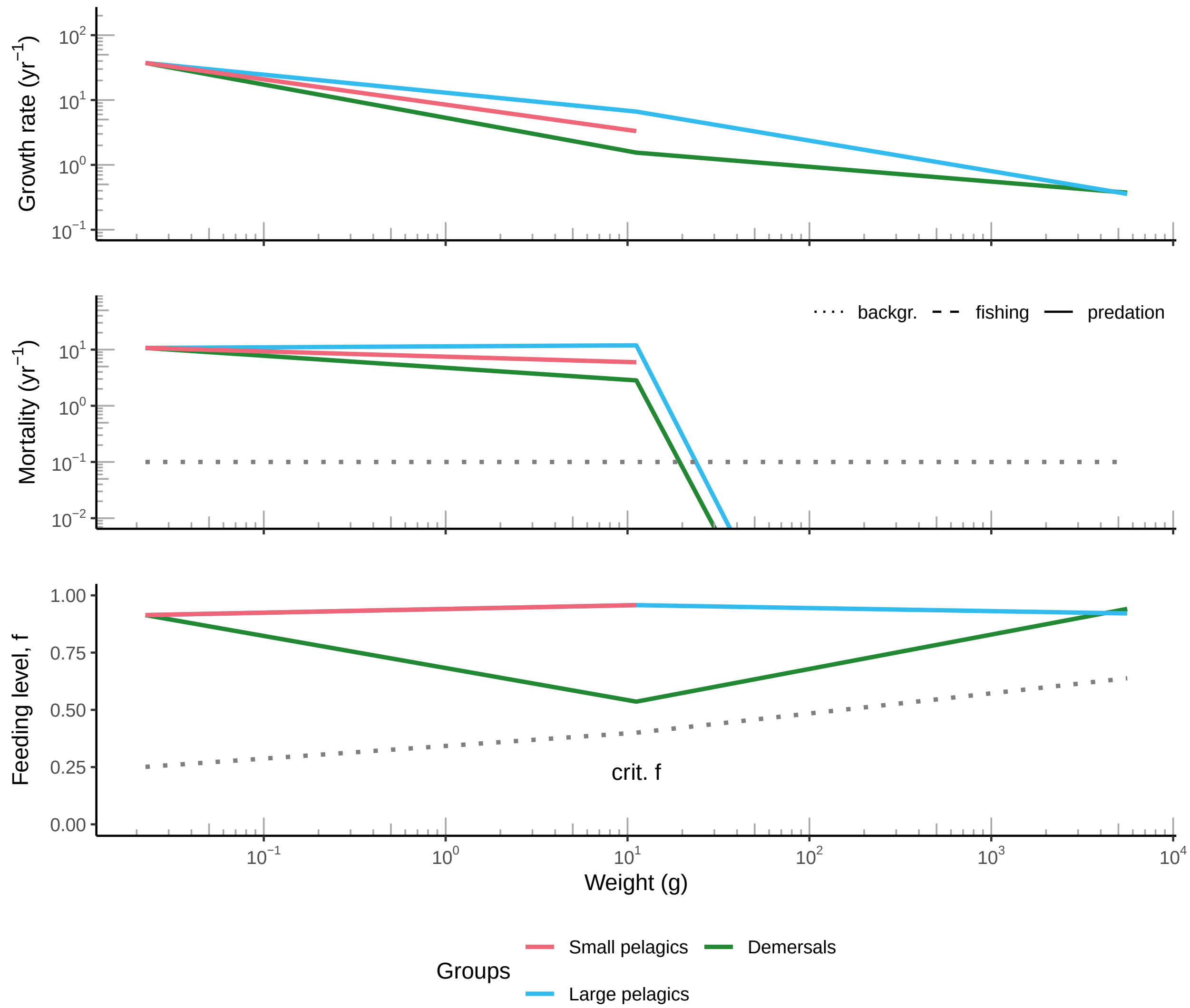


This figure collection includes `plotSpectra()`, `plotRates()`, `plotNetwork()`, and `plotBiomasstime()`. Each of these can be called independently. For instance:

```
plotBiomasstime(sim)
```




```
plotRates(sim)
```



Fishing mortality assignment

For simplicity, arguments of fishing in `setupbasic()` and `setupVertical()` only allow assigning fishing mortality to all functional types. Although the parameter set has been generated by calling setup functions e.g., `setupVertical()`, it is feasible to overwrite parameters manually. As a result, fishing mortality for a specific functional type can be assigned afterwards.

```
p=setupVertical2(szprod= 120,
                 lzprod = 120,
                 dfpho=200,
                 depth = 700,
                 nStages = 9,
                 F=0) # no fishing for all size classes
names(p$mortF)=p$stagenames
df=data.frame(mortF_original=c(p$mortF[p$ix[[1]]],p$mortF[p$ix[[5]]]))
# assign 0.2/year as the maximum fishing mortality to small pelagic fish
p=setFishing(p=p,F=0.2,etaF=0.05,groupidx=c(1))
# assign 0.3/year as the maximum fishing mortality to demersal fish
```

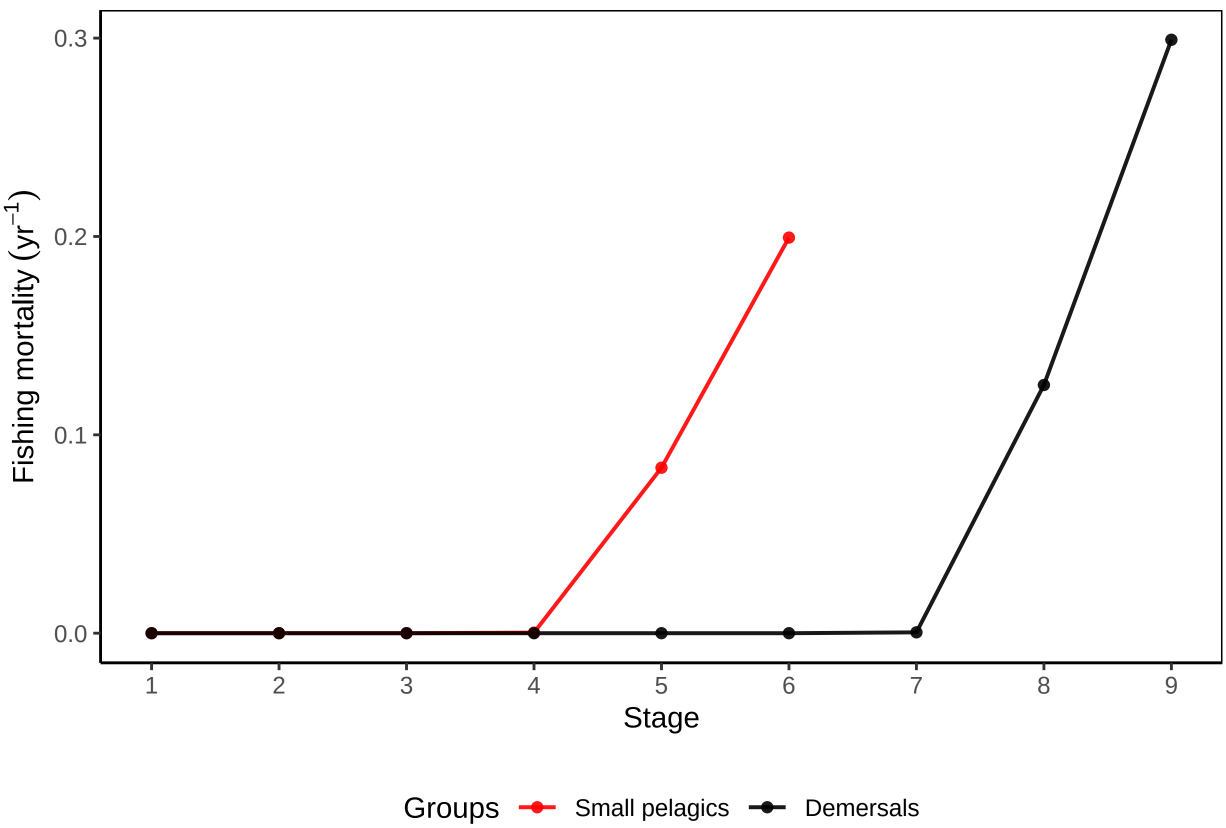
```r
p=setFishing(p=p,F=0.3,etaF=0.05,groupidx=c(5))
df=cbind(df,data.frame(mortF_new=c(p$mortF[p$ix[[1]]],p$mortF[p$ix[[5]]])))
knitr::kable(df,caption="Fishing mortality before and after assignment")
```

Table 3: Fishing mortality before and after assignment

	mortF_original	mortF_new
smallPel_1	0	0.0000000
smallPel_2	0	0.0000000
smallPel_3	0	0.0000006
smallPel_4	0	0.0002858
smallPel_5	0	0.0834188
smallPel_6	0	0.1994425
demersals_1	0	0.0000000
demersals_2	0	0.0000000
demersals_3	0	0.0000000
demersals_4	0	0.0000000
demersals_5	0	0.0000000
demersals_6	0	0.0000009
demersals_7	0	0.0004287
demersals_8	0	0.1251281
demersals_9	0	0.2991638

```r
df=data.frame("Stage"=1:length(p$ix[[1]]), "mortF"=p$mortF[p$ix[[1]]],"Groups"="smallPel")
df=rbind(df,data.frame("Stage"=1:length(p$ix[[5]]),
                       "mortF"=p$mortF[p$ix[[5]]],"Groups"="demersals"))
df$Groups=factor(df$Groups,levels=c("smallPel","demersals"))
# plot of fishing mortality of small pelagics and demersals
fig=ggplot(df, aes(x = Stage, y = mortF, color = Groups))+
    geom_line(linewidth = 0.7,alpha=0.9)+
    geom_point(size=1.5,alpha=0.9)+
  labs(x = expression("Stage"), y = expression("Fishing mortality"~(yr^{-1}))) +
  scale_color_manual(values = c("red", "black"),labels=c("Small pelagics","Demersals")) +
  scale_x_continuous(breaks = unique(df$Stage))+
      theme(panel.background = element_rect(fill = "white"),
          panel.border = element_rect(color = "black", fill = NA),
          axis.line = element_line(color = "black"),
          #legend.title = element_blank(),
          legend.key = element_rect(fill = "transparent", color = "transparent"),
          legend.position = "bottom")

fig
```

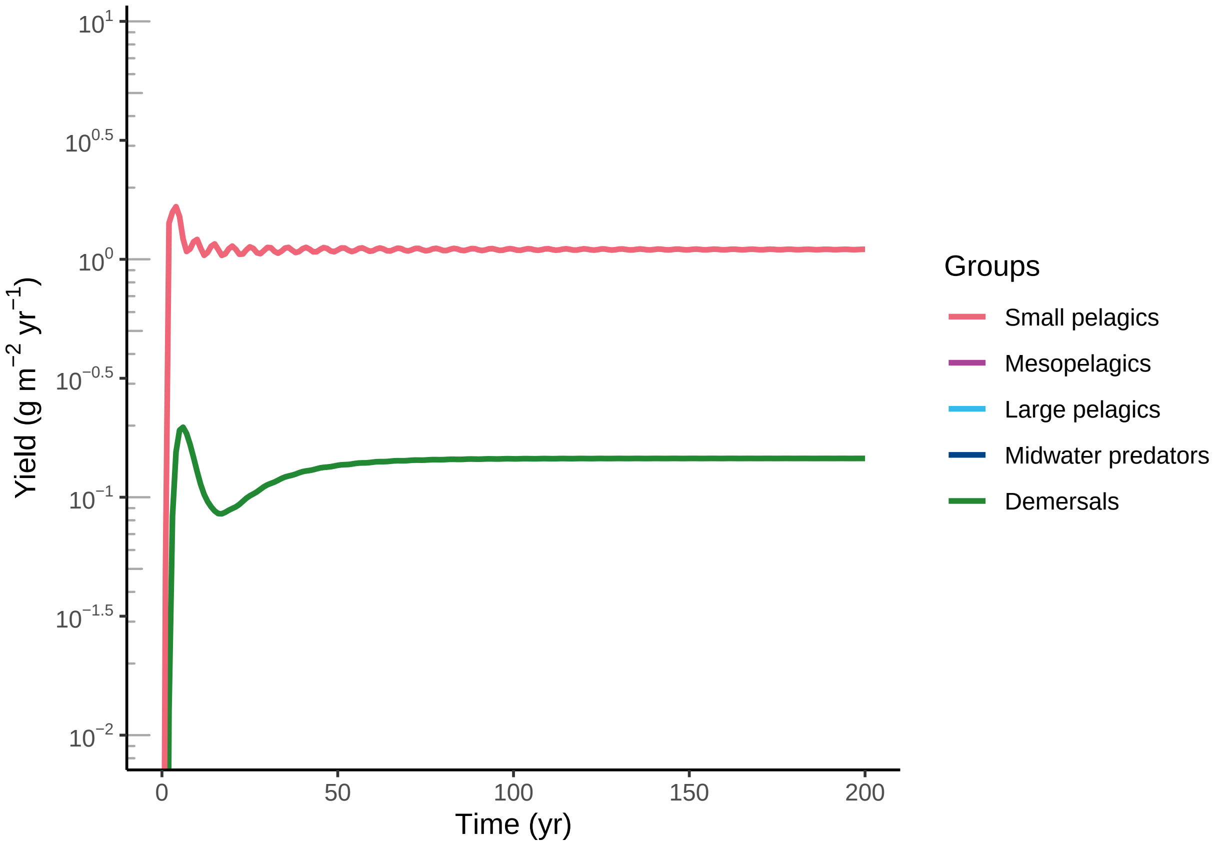


Since fishing mortality was assigned manually to two of three fish functional types, which is not the ready-to-use function `setupXXX()` can do, we must turn on `USEdll` and `bCust` flags for simulations. It means we want to run the simulation based on a parameter set we customized. All core parameters for simulation will be transmitted from R to Fortran dll rather than generated in Fortran. These two flags are TRUE as default. If `USEdll = F`, it means the simulation is done in R (slower but helpful when debugging).

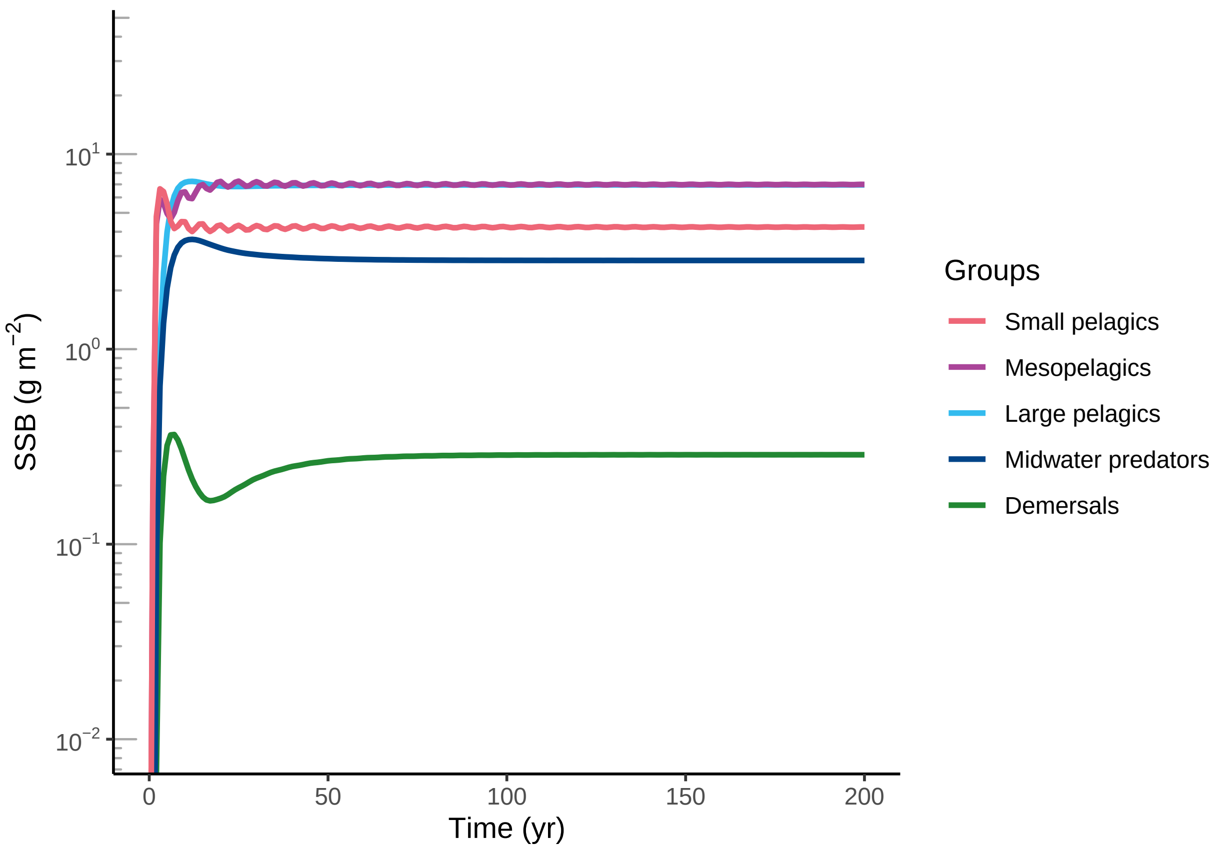
```
sim=simulateFEISTY(p = p, tEnd = 200, USEdll = T, bCust = T)
```

The following functions can be used for visualizing yield and spawning stock biomass changes over time.

```
plotYieldtime(sim)
```




```
plotSSBtime(sim)
```



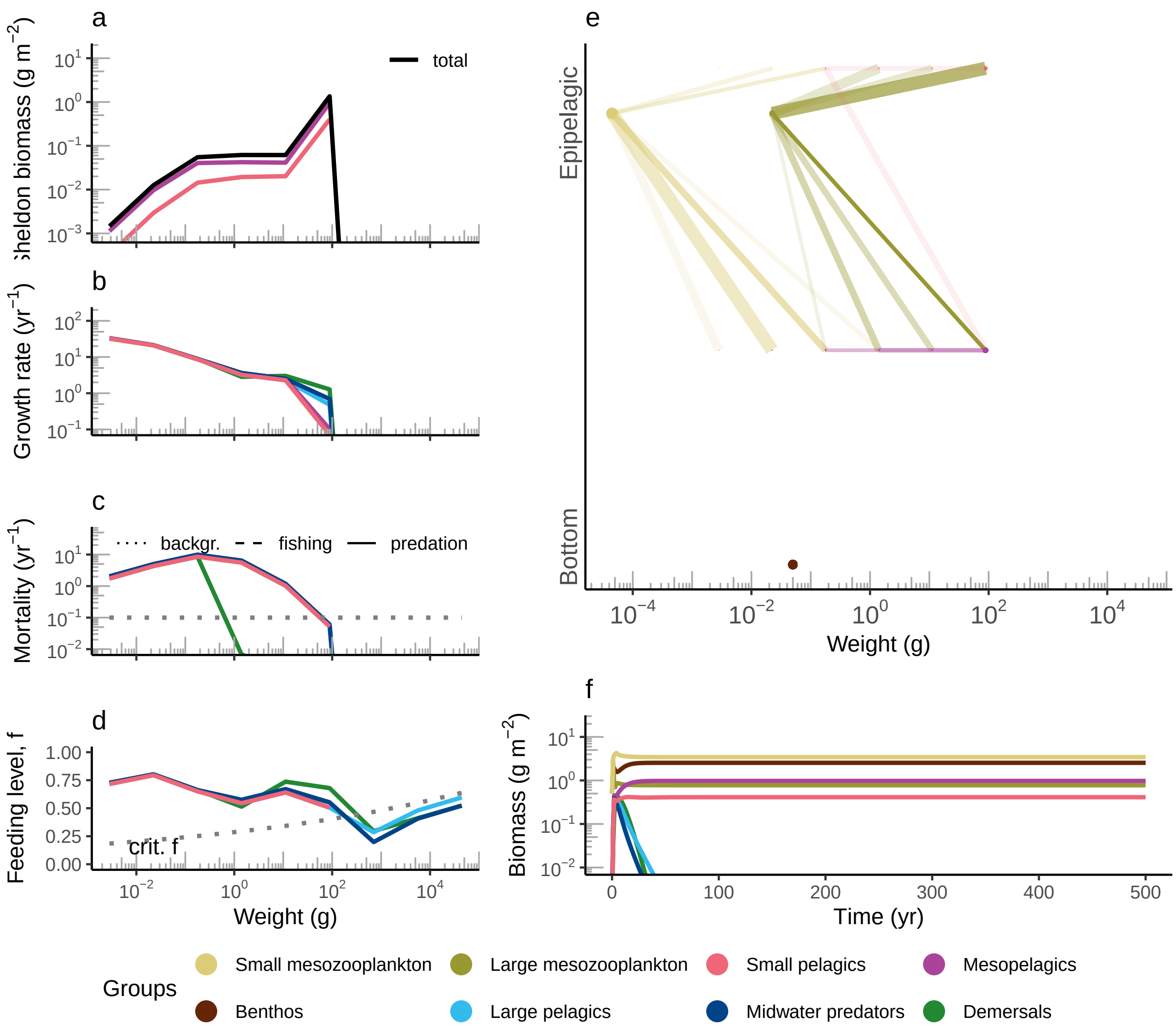
Bottom-up control examples

One of the goals of the FEISTY model is to obtain emergent fish food webs that vary with environmental conditions (i.e. bottom-up mechanisms that control fish communities). Here we demonstrate two model runs with one describing an oligotrophic system and the other one a more eutrophic system based on `setupVertical2`.

```
p1=setupVertical2(depth=1000,szprod=5, lzprod=5,dfpho = 130) # oligotrophic 1000 meter
p2=setupVertical2(depth=1000,szprod=100, lzprod=100,dfpho =380) # eutrophic 1000 meter
```

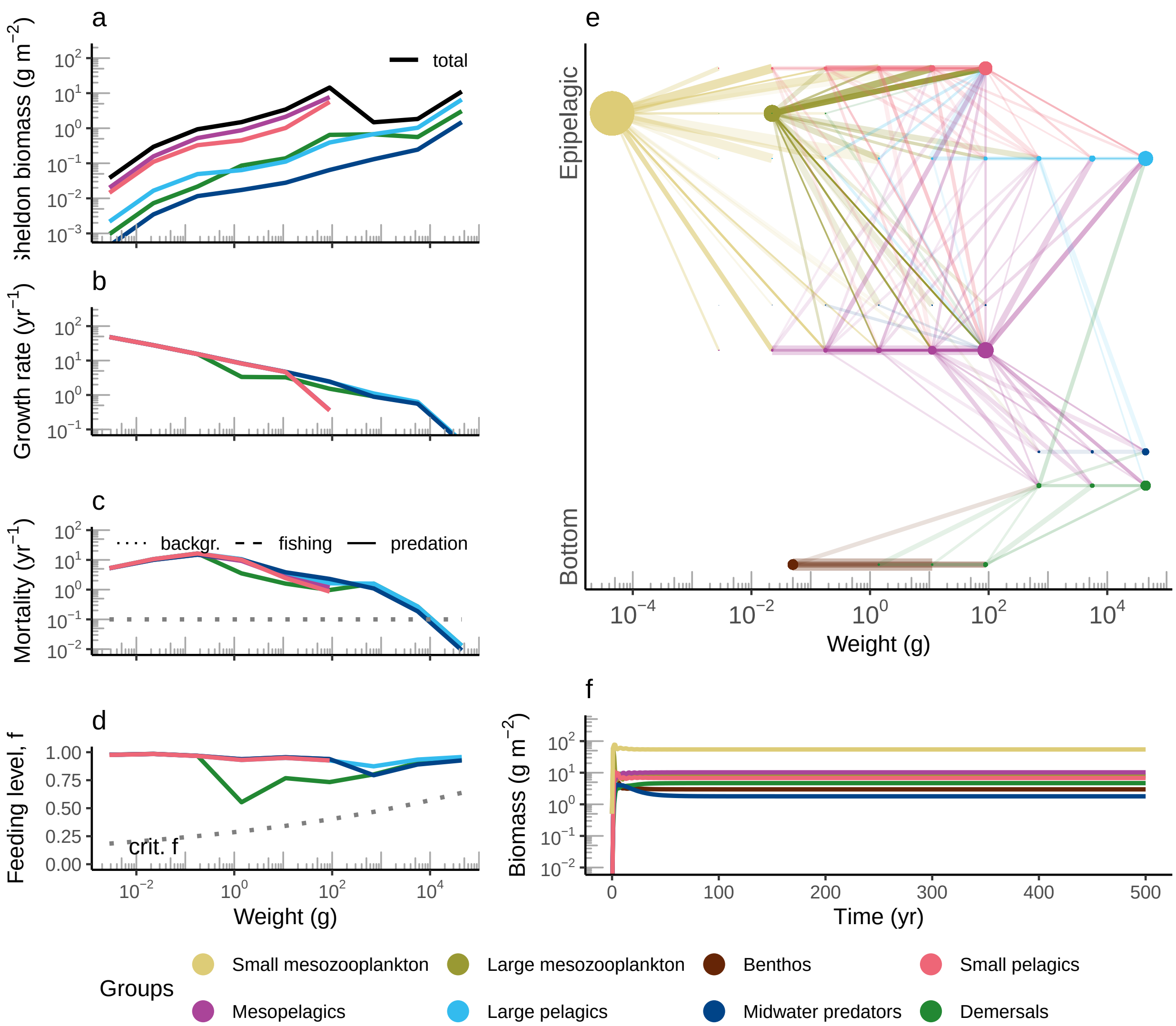
In the oligotrophic water, large pelagic fish, midwater predators, and demersal fish cannot survive (panel f), since the resource productions are low and do not provide enough food for them (panel d).

```
sim1=simulateFEISTY(p=p1,tEnd=500)
plotSimulation(sim1)
```



On the contrary, in the eutrophic water, high resource productions support the existence of all five functional types (panel f). All fish have feeding levels that are higher than their critical feeding levels (panel d).

```
sim2=simulateFEISTY(p=p2,tEnd=500)
plotSimulation(sim2)
```


a
b
c
d
e
f
total
Sheldon biomass (g m^{-2})
Growth rate (yr^{-1})
Mortality (yr^{-1})
backgr.
fishing
predation
Feeding level, f
crit. f
Weight (g)
Epipelagic
Bottom
Biomass (g m^{-2})
Time (yr)
Groups
Small mesozooplankton
Large mesozooplankton
Benthos
Small pelagics
Mesopelagics
Large pelagics
Midwater predators
Demersals

References

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