

# FishErles Size and functional TYpe model (FEISTY) in R

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2024

## Introduction

This vignette provides a comprehensive description of the model equations, parameters, and numerical implementation used in the **FEISTY** model system (Petrik et al. 2019; Denderen et al. 2021; zhao2024FEISTY?). Further, it provides a few examples at the end.

## The FEISTY model

### Biomass dynamics

#### Fish dynamics

The biomass of each size class of a functional type of fish ( $B_i$ , gWW m<sup>-2</sup>)<sup>1</sup> changes over time ( $t$ ) according to source and sink of energy (De Roos et al. 2008):

$$\frac{dB_i}{dt} = J_{in,i} + (\nu_i - \rho_i - \mu_i)B_i - J_{out,i}, \quad (1)$$

where  $\nu_i$  is the rate of available energy for growth and reproduction,  $\rho_i$  is the rate of reproduction, and  $\mu_i$  (year<sup>-1</sup>) is the total mortality rate. The size of fish increases as a result of growth. The grown flux out of the current size class enters the next size class (excluding the largest fish). The growth flux out of a size class  $i$  is

$$J_{out,i} = \gamma_i B_i, \quad (2)$$

where  $\gamma_i$  is the growth rate (year<sup>-1</sup>). The growth flux to a size class includes two parts for the smallest fish and other sizes, respectively:

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

where  $\epsilon_r$  is the reproduction efficiency. The flux into the smallest fish class ( $i = 1$ ) is from the reproduction of each size class of mature fish plus the growth flux out of the largest fish class ( $J_{out,n}$ ) because they cannot grow larger. For larger fish ( $i > 1$ ), the growth flux into the size class  $i$  is from the growth of the previous neighboring size class ( $i - 1$ ).

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<sup>1</sup>gWW: gram wet weight. From now on, we use “g” to represent “gWW” for simplicity.

## Resource dynamics

The resource  $i$  biomass evolves over time according to a chemostat-like growth and consumption by predators, which is the default resource dynamic mode in four internal setups:

$$\frac{dR_i}{dt} = r(K_i - R_i) - \mu_{p,i}R_i, \quad (4)$$

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

$$\frac{dR_i}{dt} = r_i \cdot R_i \cdot \left(1 - \frac{R_i}{K_i}\right) - \mu_{p,i} \cdot R_i, \quad (5)$$

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

## Physiological rates

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

$$C_{\max,i} = k_{T,i} \cdot a_c \cdot m_i^{b_c} \quad (6)$$

$$V_i = k_{T,i} \cdot a_e \cdot m_i^{b_e} \quad (7)$$

$$M_i = k_{TM,i} \cdot a_m \cdot m_i^{b_m} \quad (8)$$

Here  $k_{T,i}$  and  $k_{TM,i}$  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 (without temperature effects) are assigned by the `paramAddPhysiology()` function. The temperature effects on biological rates are added subsequently (see Section **Temperature effects**). Note, though, these are all done internally by the “setup” functions.

## Energy budget

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

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

where  $\epsilon_\alpha$  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:

$$f_i = \frac{E_i}{E_i + C_{\max,i}} \quad (10)$$

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 ( $\text{year}^{-1}$ )  $E_i$  of a predator  $i$  is:

$$E_i = V_i \sum_j \theta_{i,j} B_j, \quad (11)$$

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

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

$\psi_i$  is the maturity level (dimensionless) of fish  $i$ , describing the proportion of available energy ( $\nu_i$ ) 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):

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

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

$$m_{\text{mature}} = \eta_{\text{mature}} M \quad (14)$$

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

The remaining fraction of the available energy ( $\nu_i$ ) is invested in growth:

$$\kappa_i = 1 - \psi_i \quad (15)$$

Then the growth from the current size class ( $i$ ) to next neighboring size class ( $i + 1$ ) can be calculated (De Roos et al. 2008):

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

$\mu_i$  is the total mortality including the predation mortality rate ( $\mu_{p,i}$ ), background mortality rate ( $\mu_{b,i}$ ), and fishing mortality rate ( $\mu_{f,i}$ ):

$$\mu_i = \mu_{p,i} + \mu_{b,i} + \mu_{f,i} \quad (17)$$

All size classes of fish experience a background mortality. The details of predation and fishing are in the sections below.

## Predation

The second core element of FEISTY, besides the equation for biomass dynamics, is the specification of how each size class interacts via predation. This is specified in the feeding preference matrix (also known as a food-web matrix)  $\theta_{i,j}$  where each element 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 or derived from size preference coupling with the vertical habitat of each functional group. All of them are combined with additional modifications to account for feeding specializations.

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

$$\mu_{p,j} = \sum_i \frac{V_i \theta_{i,j} B_i}{E_i + C_{\text{max},i}} C_{\text{max},i} \quad (18)$$

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

$$\theta_{i,j} = \theta_{s,i,j} \cdot \theta_{v,i,j} \quad (19)$$

The calculation of  $\theta_{s,i,j}$  follows Eq. 21 in setupVertical and Eq. 20 in setupVertical2. The detailed description of  $\theta_{v,i,j}$  in the Section **Vertical overlap**.

## Size preference

In the non-vertical distribution version (`setupBasic` and `setupBasic2`)  $\theta_{i,j}$  refers to the feeding preference based on the size preference. In vertical distribution versions, 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)). It also can be calculated by following functions either based on the log-normal distribution:

$$\theta_{i,j} = \begin{cases} \exp\left(-\frac{\left(\log\left(\frac{m_{c,i}}{\beta \cdot m_{c,j}}\right)\right)^2}{(2 \cdot \sigma)^2}\right), & m_i > m_j \\ 0, & m_i \leq m_j \end{cases} \quad (20)$$

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

$$\theta_{i,j} = \frac{\sqrt{\frac{\pi}{2}} \cdot \sigma \cdot \left( \operatorname{erf}\left(\frac{\log(m_{u,j}) - \log\left(\frac{m_{c,i}}{\beta}\right)}{\sqrt{2} \cdot \sigma}\right) - \operatorname{erf}\left(\frac{\log(m_{l,j}) - \log\left(\frac{m_{c,i}}{\beta}\right)}{\sqrt{2} \cdot \sigma}\right) \right)}{\log(m_{u,j}) - \log(m_{l,j})} \quad (21)$$

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

## Vertical overlap

Concise introduction... **Daniël Please add more.**

water column discretization

$$z_\zeta = 0 + \zeta, \quad \zeta \in [0, z_b] \quad (22)$$

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

$z_{\text{dvm}}$  is the representative depth where there is max biomass when functional types or size classes conduct the diel vertical migration.

$$z_{\text{dvm}} = \begin{cases} z_{\text{photc}} + 500, & z_{\text{bottom}} \geq z_{\text{photc}} + 500 \\ z_{\text{bottom}}, & z_{\text{photc}} + 500 > z_{\text{bottom}} > z_{\text{shelf}} \\ 0, & z_{\text{bottom}} \leq z_{\text{shelf}} \end{cases} \quad (23)$$

For demersal fish, the vertical habitats are different.

$$z_{\text{dvm}} = \begin{cases} z_{\text{dvm}}, & z_{\text{bottom}} - z_{\text{dvm}} < 1200 \\ z_{\text{bottom}} - 1200, & 1200 \leq z_{\text{bottom}} - z_{\text{dvm}} < 1500 \\ z_{\text{bottom}}, & z_{\text{bottom}} - z_{\text{dvm}} \geq 1500 \end{cases} \quad (24)$$

The vertical range of the vertical distribution of each organism  $\omega_i$  increases with body mass:

$$\omega_i = \omega_0 + \tau \cdot \log_{10}\left(\frac{m_{c,i}}{m_{c,0}}\right) \quad (25)$$

where  $\omega_0$  is the baseline range of the vertical distribution and  $\tau$  is the range-increasing factor of vertical distribution.  $m_{c,0}$  denotes the minimum geometric mean size within all organisms in the simulation (typically small mesozooplankton). Note, for benthic resources,  $\omega_i = \omega_0$  to constrain them to the bottom.

a function to generate vertical distributions (a normal distribution).....

$$\theta_{\zeta,x,i} = \frac{1}{\sqrt{2\pi\omega_i^2}} \cdot \exp\left(-\frac{(z_\zeta - z_{\text{loc},x,i})^2}{2\omega_i^2}\right) \quad (26)$$

$$\theta_{\zeta,x,i} = \frac{\theta_{\zeta,x,i}}{\sum_{\zeta} \theta_{\zeta,x,i}} \quad (27)$$

$x$  is either day or night.  $z_{\text{loc},x,i}$  is the representative depth that the maximum biomass is. Some functional types or size classes have two representative depths  $z_{\text{loc},x,i}$ . Consequently, they need to be calculated twice (Eq. 26 and 27) and the vertical distribution is the averaged value, which shows a bimodal shape of the vertical distribution. The description of  $z_{\text{loc},x,i}$  of different functional types and size classes can be found in (. . . . .).

#### Predator-prey vertical overlap

The less value between vertical distribution values of a specific predator  $i$  and a prey  $j$  at depth  $\zeta$  at daytime or nighttime  $x$   $\min(\theta_{\zeta,x,i}, \theta_{\zeta,x,j})$  represents their vertical overlap level. The depth-integration gives the synthetic vertical overlap value of predator  $i$  to a prey  $j$  at day or night  $\theta_{v,x,i,j}$ :

$$\theta_{v,x,i,j} = \sum_{\zeta} \min(\theta_{\zeta,x,i}, \theta_{\zeta,x,j}) \quad (28)$$

The light conditions of a location where visual predators stay in a water column influence their prey-capturing performances. Small pelagics 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. These traits are reflected by the modified vertical overlap values. Therefore, according to habitats at day and night (Table 1) the vertical overlap data is further modified by multiplying the visual scaling factor  $\theta_{\text{visual}}$ :

$$\theta_{v,x,i,j} = \theta_{v,x,i,j} \cdot \theta_{\text{visual}}. \quad (29)$$

All small pelagics and small- and medium-size class <sup>2</sup> large pelagics always stay at the surface regardless of day and night, so their daytime vertical overlap on all prey ( $\theta_{v,\text{day},i,j}$ ) is enhanced ( $\theta_{\text{visual}} = 1.5$ ). Correspondingly, their nighttime vertical overlap ( $\theta_{v,\text{night},i,j}$ ) is decreased ( $\theta_{\text{visual}} = 0.5$ ).

Half of large-size class large pelagics stay at the twilight zone ( $z_{\text{dvm}}$ ) at daytime, so their vertical overlap at daytime ( $\theta_{v,\text{day},i,j}$ ) on all mesopelagic fish and bathypelagic fish is reduced ( $\theta_{\text{visual}} = 0.5$ ).

Ultimately, the total vertical overlap is the average value of day and night vertical overlap values.

$$\theta_{v,i,j} = \frac{\theta_{v,\text{day},i,j} + \theta_{v,\text{night},i,j}}{2} \quad (30)$$

This can be used for the calculation of feeding preference ( $\theta_{i,j}$ ) in Eq. 19. Note  $\theta_{i,j}$  still needs to be further modified according to feeding behaviours (see Section **Modification**).

#### Zooplankton resources

Zooplankton resources (small and large mesozooplankton) are supposed to be divided into two types in terms of whether they can conduct the diel vertical migration if water column conditions allow. During the daytime, half of them move to deep water to avoid predation ( $z_{\text{loc},\text{day},i} = z_{\text{dvm}}$ ). Another half is in the surface water ( $z_{\text{loc},\text{day},i} = 0$ ). At nighttime, they stay at the surface ( $z_{\text{loc},x,i} = 0$ ).

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

### *Benthic resources*

Benthos is benthic-living ( $z_{\text{loc},\text{day},i} = z_{\text{loc},\text{night},i} = z_{\text{bottom}}$ ). To ensure they stay close to the sea floor, their vertical distribution width is kept as the baseline value  $\omega_i = \omega_0$ .

### *Small pelagics*

They always stay in the surface water ( $z_{\text{loc},\text{day},i} = z_{\text{loc},\text{night},i} = z_{\text{bottom}}$ ).

### *Mesopelagics*

Mesopelagic fish stay at the midwater during daytime ( $z_{\text{loc},\text{day},i} = z_{\text{dvm}}$ ). At night, they migrate to the surface ( $z_{\text{loc},\text{night},i} = 0$ ).

### *Large pelagics*

During the daytime, Large pelagics perform differently according to their size. The small- and medium-size classes are at the surface ( $z_{\text{loc},\text{day},i} = 0$ ). The large-size classes are divided into two groups: half of them are always in the surface water ( $z_{\text{loc},\text{day},i} = 0$ ), and half in midwater ( $z_{\text{loc},\text{day},i} = z_{\text{dvm}}$ ). They all move to the surface during night ( $z_{\text{loc},\text{night},i} = 0$ ).

### *Bathypelagics*

All bathypelagic fish stay at the dvm depth during daytime ( $z_{\text{loc},\text{day},i} = z_{\text{dvm}}$ ). At night, the small- and medium-size classes are always at the surface ( $z_{\text{loc},\text{night},i} = 0$ ). Large-size classes are in midwater ( $z_{\text{loc},\text{night},i} = z_{\text{dvm}}$ ).

### *Demersals*

During daytime, small demersals are at the surface ( $z_{\text{loc},\text{day},i} = 0$ ); medium demersals are at the bottom ( $z_{\text{loc},\text{day},i} = z_{\text{bottom}}$ ); large demersals are at midwater ( $z_{\text{loc},\text{day},i} = z_{\text{dvm}}^{\text{dem}}$ ). At night, small demersal fish are at the surface ( $z_{\text{loc},\text{night},i} = 0$ ). Medium and large demersal fish are at the bottom ( $z_{\text{loc},\text{night},i} = z_{\text{bottom}}$ ).

Table 1: Biomass representative depth for each size class  $z_{\text{loc},x,i}$  at day and night.  $z_{\text{dvm}}$  and  $z_{\text{dvm}}^{\text{dem}}$  can be found in Eq. 23 and 24.

Resources	Day			Night		
Zooplankton <sup>a</sup>	0 and $z_{\text{dvm}}$			0		
Benthos	$z_{\text{bottom}}$			$z_{\text{bottom}}$		
Fish	Small	Medium	Large	Small	Medium	Large
Small pelagic fish	0	0	/	0	0	/
Mesopelagic fish	$z_{\text{dvm}}$	$z_{\text{dvm}}$	/	0	0	/
Large pelagic fish	0	0	0 and $z_{\text{dvm}}$	0	0	0
Bathypelagic fish	$z_{\text{dvm}}$	$z_{\text{dvm}}$	$z_{\text{dvm}}$	0	0	$z_{\text{dvm}}$
Demersal fish	0	$z_{\text{bottom}}$	$z_{\text{dvm}}^{\text{dem}}$ <sup>b</sup>	0	$z_{\text{bottom}}$	$z_{\text{bottom}}$ <sup>e</sup>

<sup>a</sup> Zooplankton include small and large mesozooplankton

<sup>b</sup> If the water column is shallower than the photic zone depth ( $z_{\text{bottom}} < z_{\text{photic}}$ ), large demersal fish migrate over the water column (two  $z_{\text{loc},x,i}$  for each day and night:  $z_{\text{dvm}}^{\text{dem}}$  and  $z_{\text{bottom}}$ ), resulting a normal distribution centered at the middle of the water column. In such cases,  $z_{\text{dvm}}^{\text{dem}} = 0$ .

## Modifications

### Basic2

The feeding preference is further modified to facilitate the coexistence of various functional types. Here we show 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 a reduced feeding preference for 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 ( $< 200$  m), large demersal fish swim over the water column, meaning they can eat both pelagic and benthic organisms. However, we assume that they are less efficient at attacking pelagic prey and hence their feeding preference on forage fish is down-regulated:  $\theta_A \cdot \theta_D \cdot \theta_{i,j}$ ; similarly for their feeding preference on large pelagic fish:  $\theta_D \cdot \theta_{i,j}$ . In deeper waters ( $> 200$  m), 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 and Vertical2**

It is assumed all pelagic functional types (forage fish, mesopelagics, large pelagics, and bathypelagics) and small demersal fish (pelagic-living) do not consume benthos ( $\theta_{i,j} = 0$ ). Also, their feeding preference on medium demersal fish (benthic-living) is reduced by multiplying 0.25 ( $\theta_{i,j} = \theta_{i,j} \cdot 0.25$ ). Medium and large demersal fish are assumed not to eat zooplankton ( $\theta_{i,j} = 0$ ). To maintain the coexistence between large pelagic predators and small fish, some benefits in predation avoidance are assigned to medium-size forage fish and medium-size mesopelagic fish by a similar method in (Petrík et al. 2019). Large-size classes of pelagic-living functional fish groups (large pelagic fish, bathypelagic fish, and demersal fish) have reduced feeding preference on medium-size forage fish and medium-size mesopelagic fish ( $\theta_{i,j} = \theta_{i,j} \cdot 0.5$ ).

### **Fishing mortality**

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 (Andersen 2019, chap. 5):

$$\mu_{f,i} = \psi_{f,i} F_{\max} \quad (31)$$

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

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

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

$$m_{\text{fishing}} = \eta_F M \quad (33)$$

where  $\eta_F$  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:

$$k = Q_{10}^{\frac{T - T_{\text{ref}}}{10}} \quad (34)$$

where  $T_{\text{ref}}$  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). Through introducing different  $Q_{10}$  coefficients (Table 2), various temperature scaling factors  $k$  can be obtained.  $k_T$  is the temperature scaling factor for  $C_{\text{max},i}$ , and  $V_i$ ;  $k_{\text{TM}}$  is the temperature scaling factor for  $M_i$ .

### setupBasic and setupBasic2

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 ( $> 200$  m). However, in shallow water ( $< 200$  m), due to their better swimming abilities, the large demersals migrate over the water column for feeding. 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`. Moreover, to better describe the temperature effects on large demersals, the effective temperature is introduced (see Section **Real-time effective temperature**).

### setupVertical

In `setupVertical`, fish have a new trait axis of 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:

$$\theta_{\zeta,i} = \frac{\theta_{\zeta,\text{day},i} + \theta_{\zeta,\text{night},i}}{2} \quad (35)$$

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

$$k_{\zeta,i} = \theta_{\zeta,i} \cdot Q_{10}^{\frac{T_{\zeta} - T_{\text{ref}}}{10}} \quad (36)$$

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.

$$k_i = \sum_{\zeta} k_{\zeta,i} \quad (37)$$

$k_i$  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`. The effective temperature of different size classes of each functional type are the averaged values of temperatures of their approximate vertical positions of day ( $T_{\text{day}}$ ) and night ( $T_{\text{night}}$ ).

$$T_e = \frac{T_{\text{day}} + T_{\text{night}}}{2} \quad (38)$$

Note this  $T_e$  is different from the one in the Section **Real-time effective temperature**. Then  $T_e$  is taken into Eq. 34 as  $T$ , and so the temperature-dependent physiological rates (Eq. 6, 7, 8) are updated. The implementation is hard-coded in the function `setupVertical2()`.



### *Small pelagics*

They always stay in the pelagic water ( $T_{\text{day}} = T_{\text{night}} = T_{\text{p}}$ ).

### *Mesopelagics*

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

$$T_{\text{day}} = \begin{cases} T_{\text{m}}, & z_{\text{dvm}} \neq z_{\text{bottom}} \text{ and } z_{\text{dvm}} \neq 0 \\ T_{\text{b}}, & z_{\text{dvm}} = z_{\text{bottom}} \\ T_{\text{p}}, & z_{\text{dvm}} = 0 \end{cases} \quad (39)$$

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

### *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.

$$T_{\text{day}} = \begin{cases} \frac{T_{\text{m}} + T_{\text{p}}}{2}, & z_{\text{dvm}} \neq z_{\text{bottom}} \text{ and } z_{\text{dvm}} \neq 0 \\ \frac{T_{\text{b}} + T_{\text{p}}}{2}, & z_{\text{dvm}} = z_{\text{bottom}} \\ T_{\text{p}}, & z_{\text{dvm}} = 0 \end{cases} \quad (40)$$

All the large pelagics in non-large sizes (small and medium) are in pelagic water the during daytime ( $T_{\text{day}} = T_{\text{p}}$ ).

During nighttime, all of them regardless of size are in the pelagic water ( $T_{\text{night}} = T_{\text{p}}$ ).

### *Bathypelagics*

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

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

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

$$T_{\text{night}} = \begin{cases} T_{\text{m}}, & z_{\text{dvm}} \neq z_{\text{bottom}} \text{ and } z_{\text{dvm}} \neq 0 \\ T_{\text{b}}, & z_{\text{dvm}} = z_{\text{bottom}} \\ T_{\text{p}}, & z_{\text{dvm}} = 0 \end{cases} \quad (42)$$

### *Demersals*

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.

$$T_{\text{day}} = \begin{cases} T_{\text{m}}, & (z_{\text{bottom}} - z_{\text{dvm}}) < 1500 \text{ and } z_{\text{bottom}} \geq z_{\text{photic}} \\ T_{\text{b}}, & (z_{\text{bottom}} - z_{\text{dvm}}) \geq 1500 \\ \frac{T_{\text{b}} + T_{\text{p}}}{2}, & z_{\text{bottom}} < z_{\text{photic}} \end{cases} \quad (43)$$

$$T_{\text{night}} = \begin{cases} T_{\text{b}}, & z_{\text{bottom}} \geq z_{\text{photic}} \\ \frac{T_{\text{b}} + T_{\text{p}}}{2}, & z_{\text{bottom}} < z_{\text{photic}} \end{cases} \quad (44)$$

## Real-time effective temperature

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

$$\lambda = \frac{B_{\text{pelprey}}}{B_{\text{allprey}}} \quad (45)$$

where  $B_{\text{pelprey}}$  denotes the total biomass of pelagic prey for large demersal fish,  $B_{\text{allprey}}$  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:

$$T_e = T_p \cdot \lambda + T_b \cdot (1 - \lambda) \quad (46)$$

$T_e$  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()`.

## 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:

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

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 ( $m_{b,i}$ ), including all lower boundary sizes ( $m_{l,i}$ ) and upper boundary sizes ( $m_{u,i}$ ).

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

$$m_{l,i} = m_{b,i}, \quad i \in [1, n] \quad (49)$$

$$m_{u,i} = m_{b,i+1}, \quad i \in [1, n] \quad (50)$$

The geometric mean size of each size class  $m_i$  is:

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

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 <sup>a</sup>				Unit
		B1	B2	V1	V2	
$a_c$	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		$m^2 g^{-b_e-1} yr^{-1}$
$b_e$	Exponent for mass-specific clearance rate			-0.2		/
$a_m$	Intercept for mass-specific metabolism rate			$0.2 * a_c$		$g^{-b_m} yr^{-1}$
$b_m$	Exponent for mass-specific metabolism rate			-0.175		/
$\epsilon_\alpha$	Assimilation efficiency			0.7		/
$\epsilon_r$	Reproduction efficiency			0.01		/
$\mu_b$	Background mortality			0.1		$yr^{-1}$
$F_{max}$	Maximum fishing mortality rate			$0^b$		$yr^{-1}$
$\eta_{mature}$	half-maturation size coefficient	$/^c$		0.25		/
$\eta_{fishing}$	half-harvesting size coefficient	$/^d$		0.05		/
$\theta_A$	Large fish preference on forage fish <sup>d</sup>		0.5	/	/	/
$\theta_D$	Large demersal fish preference on pelagic prey		0.75	/	/	/
$\omega_0$	baseline range of the vertical distribution		/		10	/
$\tau$	range-increasing factor of vertical distribution		/		10	/
$T_{ref}$	reference temperature			10		$^{\circ}C$
$Q_{10}$	Rate of change for every 10 $^{\circ}C$ increase for clearance rate and maximum consumption			1.88		/
$Q_{10m}$	Rate of change for every 10 $^{\circ}C$ increase for metabolism		2.35		1.88	/
$aaa$	xxx	0.1	0.2	0.3	0.4	g
$\beta$	Preferred predator:prey mass ratio	/		400		/
$\sigma$	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

<sup>a</sup> B1: setupBasic1, B2: setupBasic2, V1: setupVertical1, V2: setupVertical2.

<sup>b</sup> 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  $0.3 yr^{-1}$ .

<sup>c</sup> Maturity level  $\psi_i$  is assigned manually in default B1. Only the last stage of each functional type has a value of 0.5 others are 0.

<sup>d</sup> Fishing mortality  $\mu_{f,i}$  is 0 in default B1.

<sup>e</sup> In B1,  $\theta_A$  only poses on medium forage fish (the second size class). In B2,  $\theta_A$  works on all forage fish.

## Demonstration

### The structure of main parameters

**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:

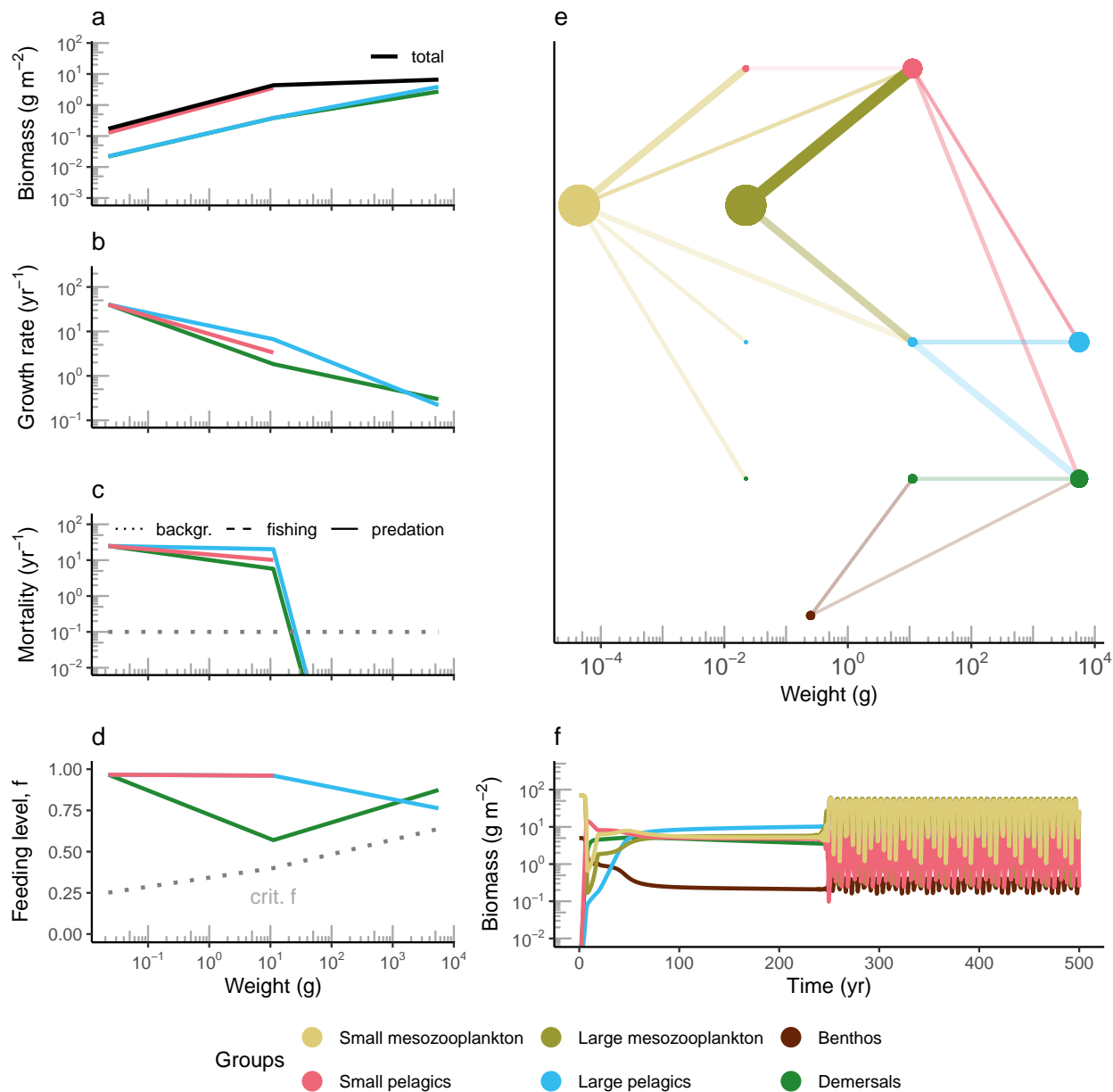
```
p <- setupBasic(szprod = 70, # small mesozooplankton production
               lzprod = 70, # large mesozooplankton production
               bprodin = 5, # benthos production
               depth = 150, # water column depth [m]
               Tp = 17, # pelagic layer averaged temperature [Celsius]
               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)
```

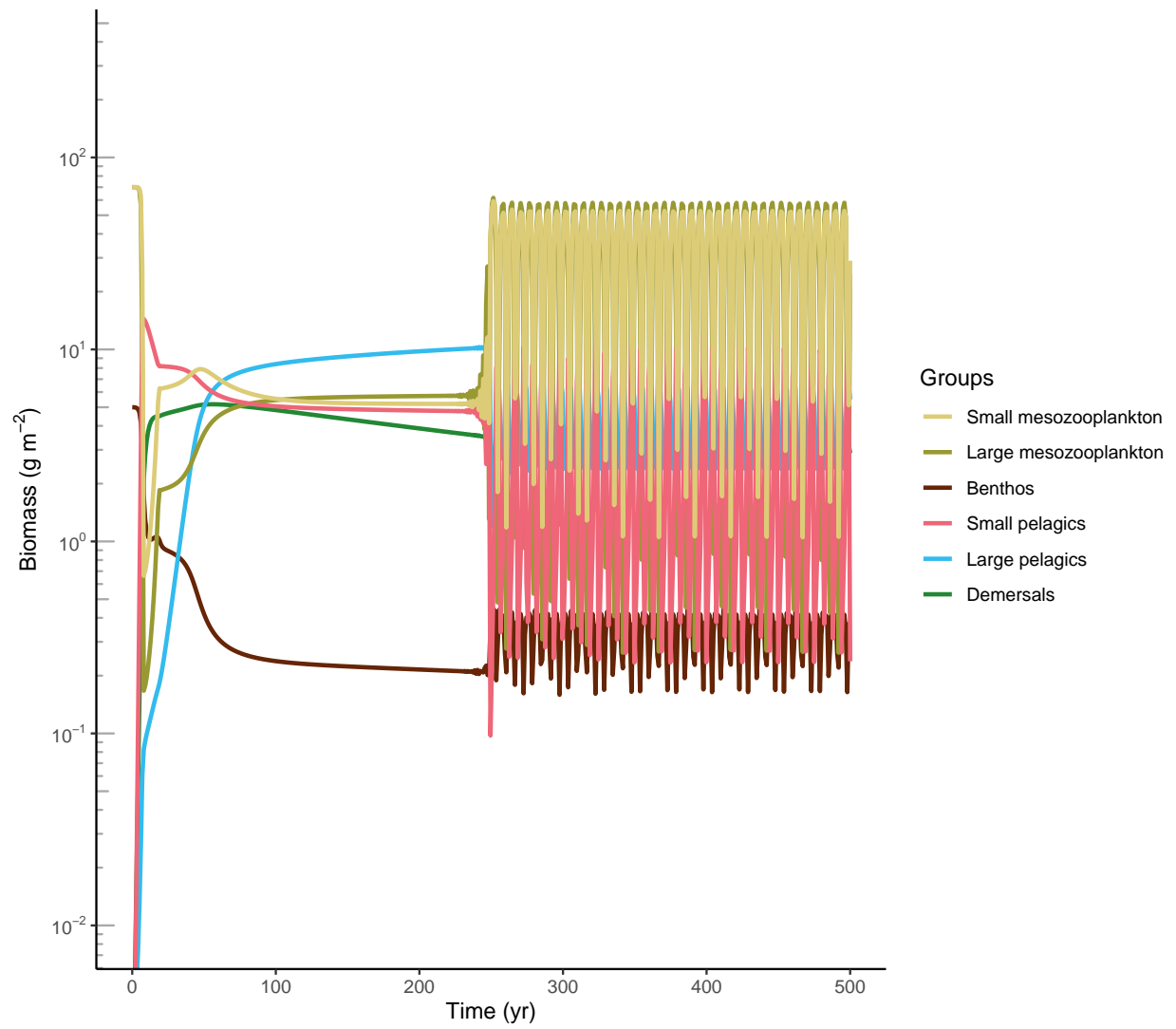
This simulation runs 500 years based on the parameter set `p` we defined above and the time series output is in every year. `USEdll = T` denotes an almost identical parameter will be generated in the Fortran dll based on the arguments provided in `setupBasic()` and the core computation will be done by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

```
plotSimulation(sim)
```

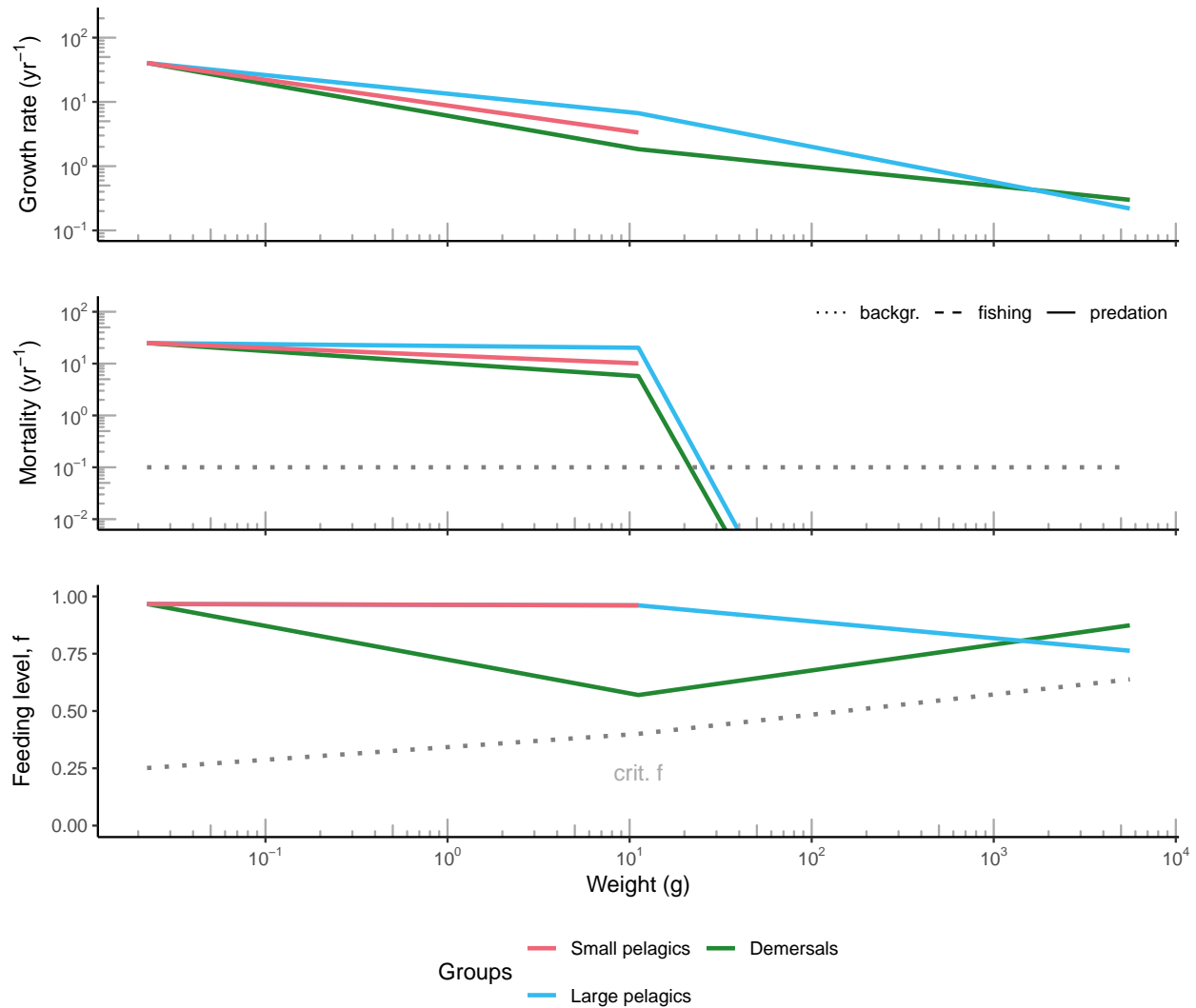


This figure collection includes `plotSpectra()`, `plotRates()`, `plotNetwork()`, and `plotBiomassTime()`. Each of these can be called independently. For instance:

```
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, we can assign fishing mortality for a specific functional type afterward.

```
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,groupid=c(1))
# assign 0.3/year as the maximum fishing mortality to demersal fish
```

```

p=setFishing(p=p,F=0.3,etaF=0.05,grouppid=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

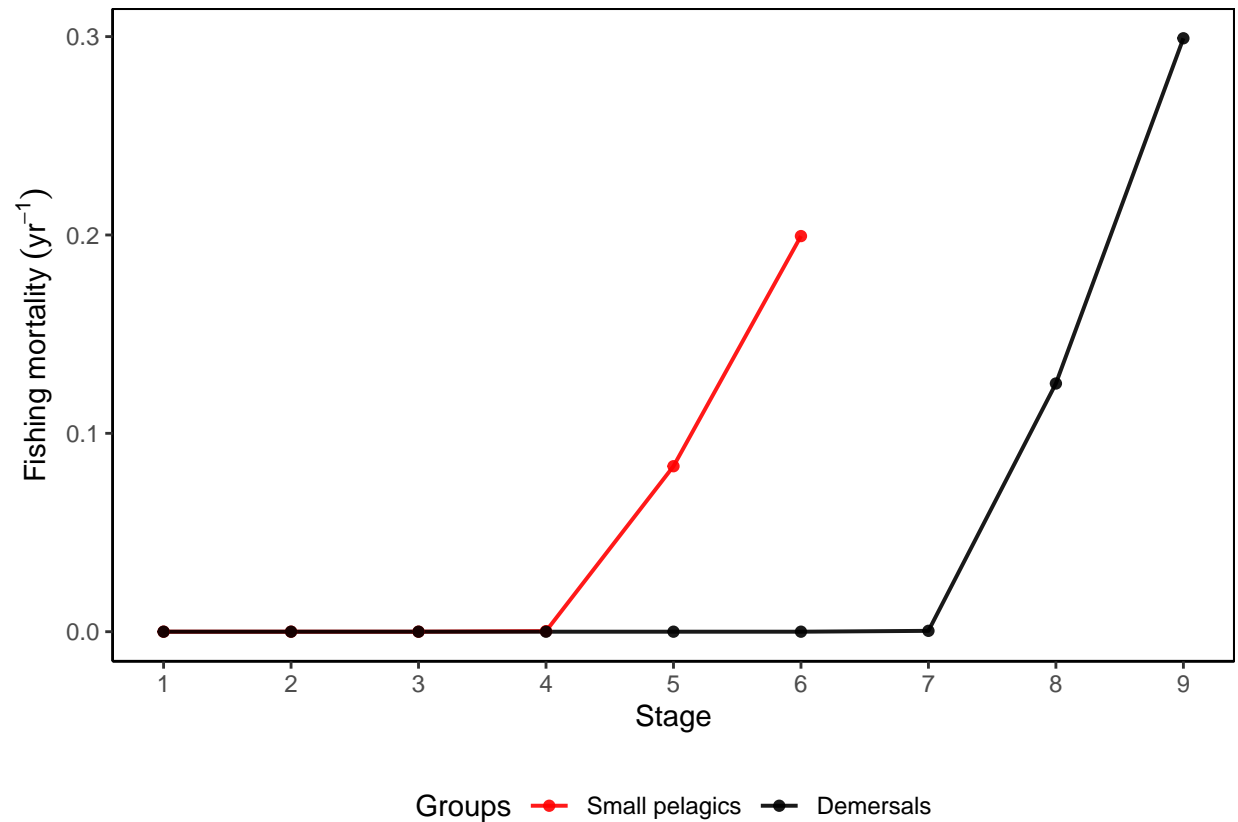
```

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

```



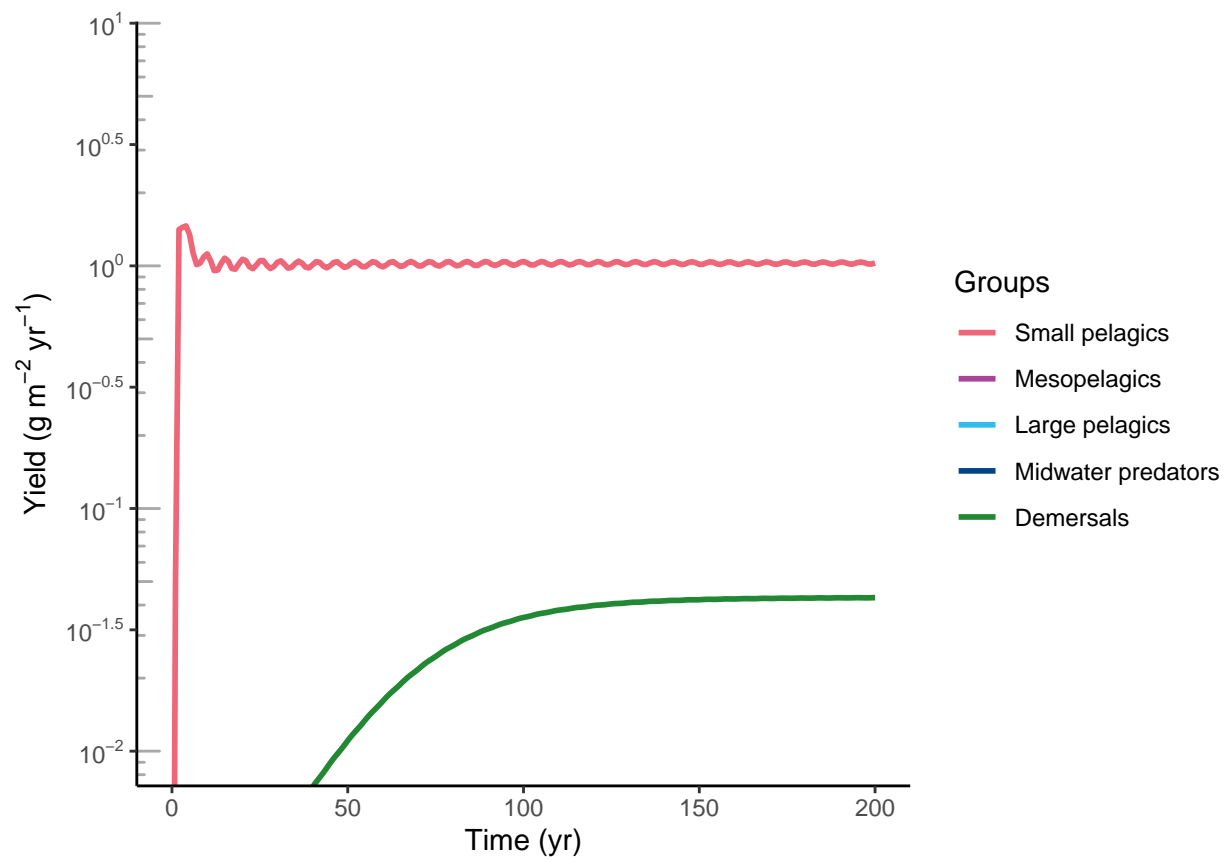


Note since we manually changed the parameter set generated by the ready-to-use function `setupXXX()`, here we must use `bCust = T`, which means we want to run the simulation based on a parameter set we customized. The only difference from `USEdll = T` is that all core parameters for simulation will be transmitted from R to Fortran dll rather than generated in Fortran.

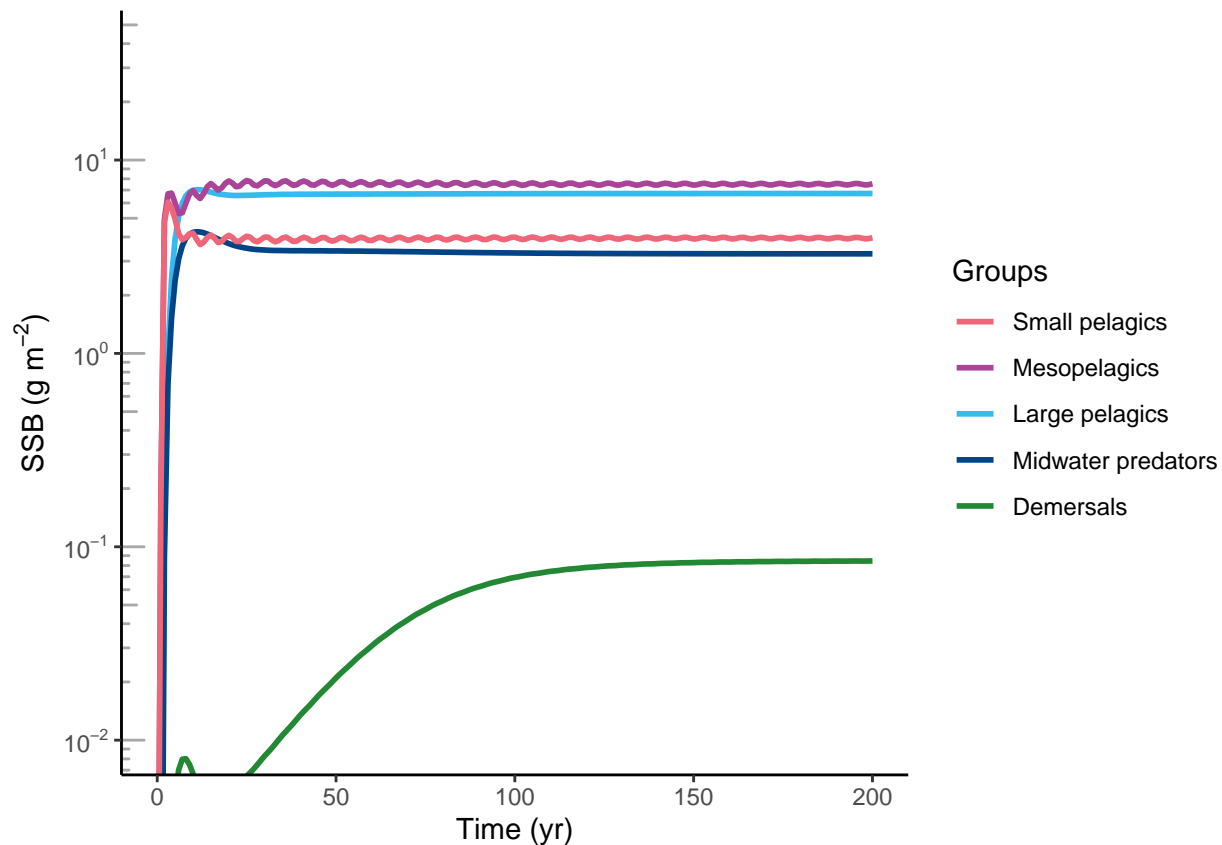
```
sim=simulateFEISTY(p = p, tEnd = 200, bCust = T)
```

There are ready-to-use functions to visualize fishery-related results. They display yield and spawning stock biomass changes over time.

```
plotYieldtime(sim)
```



```
plotSSBtime(sim)
```



## Bottom-up control examples

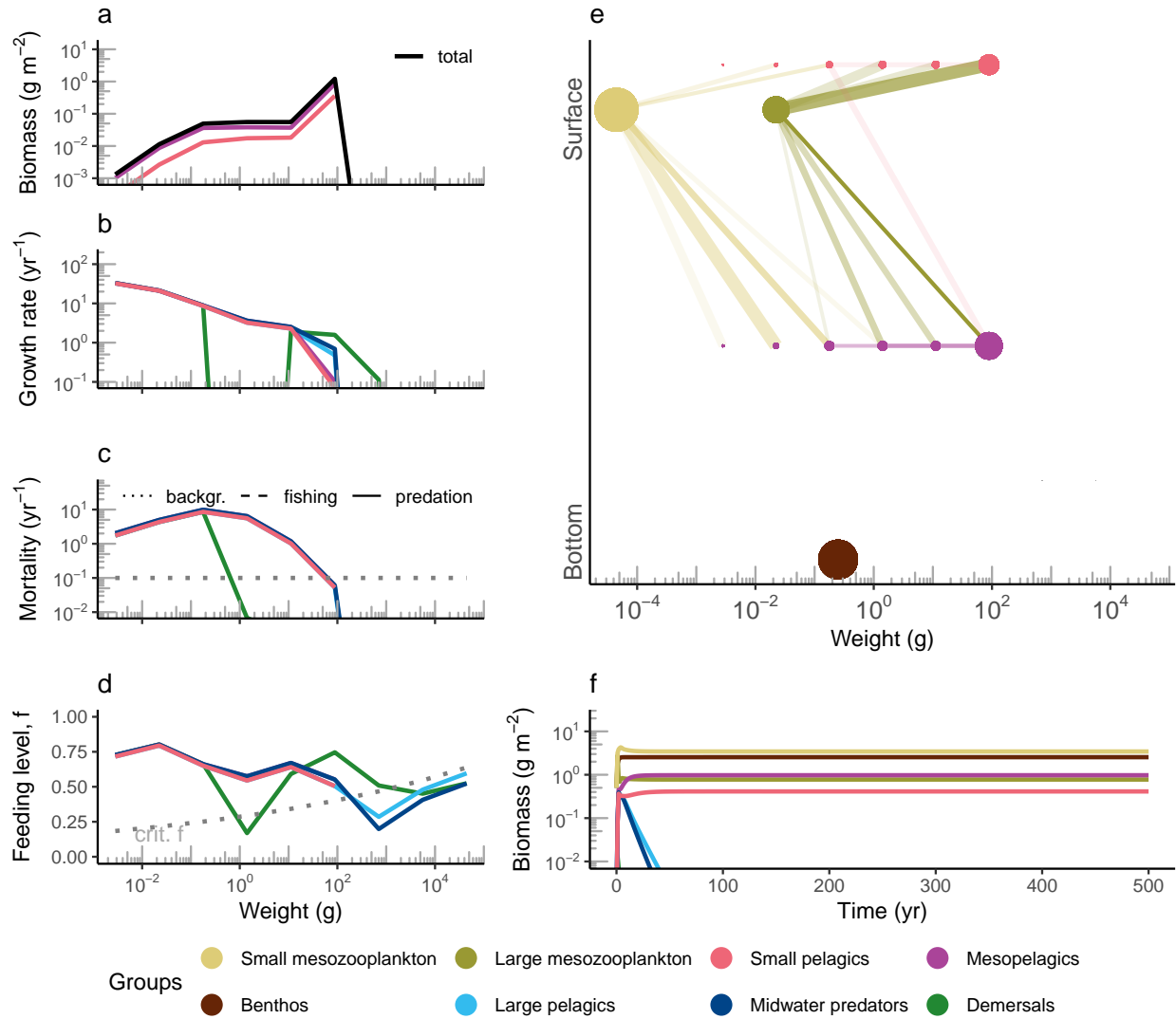
Daniël Please add more.

One of main objectives of FEISTY model is illustrating the bottom-up mechanisms of fish communities. Here we demonstrate two setups with oligotrophic conditions eutrophic conditions 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
```

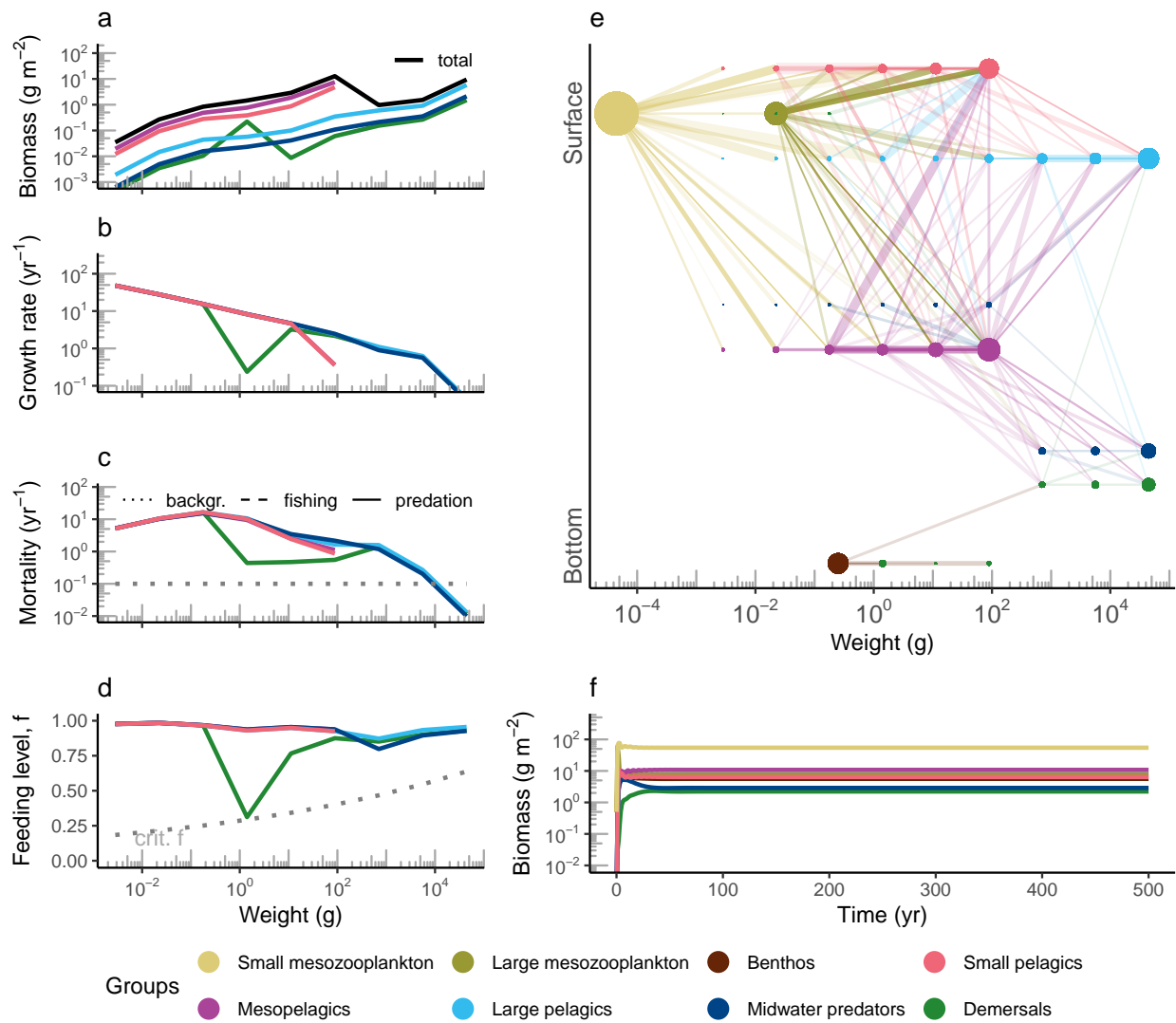
In the oligotrophic water, small pelagic fish, midwater predators, and demersal fish cannot survive (panel f), since the resource productions are low and cannot provide enough food for them (panel d).

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



On the contrary, in the eutrophic water, high resource productions can support the existence of all five functional types albeit the water is deep (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)
```



## References

- Andersen, Ken H. 2019. *Fish Ecology, Evolution, and Exploitation: A New Theoretical Synthesis*. Princeton University Press.
- 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.