Multispecies, trait-based and community size spectrum ecological modelling in R (mizer)*

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¹This document is included as a vignette (a IATEX document created using the R package knitr) of the package mizer. It is automatically downloaded together with the package and can be accessed through R typing vignette("mizer_vignette").

1 Summary

Size spectrum ecological models have emerged as a conceptually simple way to model a large community of individuals that grow and change trophic level during their lives. They are a subset of physiologically structured models where growth (and thus maturation) is food dependent, and processes are formulated in terms of individual level processes. A key feature is that of a *size spectrum*, where the total abundance of individuals at size scales negatively with size: there are more small things than big things.

mizer is a software package for implementing size spectrum ecological models using the R statistical programming environment. The package has been developed to model marine ecosystems that are subject to fishing.

Roughly speaking there are three versions of the size spectrum modelling framework of increasing complexity: The *community* model, in which only one "species" is resolved; the *trait-based* model, in which all the species-specific parameters are the same, except for the asymptotic size which determines other life-history parameters such as the size at maturity; and the *multispecies* model in which multiple "real" species are resolved, each of which can have differing species-specific traits. The community and trait-based models can be considered as simplifications of the multispecies model. mizer is able to implement all three model versions using the same set of tools.

mizer contains routines and methods to allow users to set up the model community, and then project it through time under different fishing strategies. The results of the simulations can then be explored using a range of plots and summary methods, including plots of size spectra and the calculation of community indicators such as mean weight in the community and the the slope of the size spectrum.

The models created can be quite flexible and there are many options for setting up and running simulations. For example, different stock-recruitment relationships can be implemented and fishing gears with different selectivity patterns can be set up so that different species are caught by different gears. However, mizer aims to make setting up the models relatively simple. For example, easy to use "wrapper" functions are provided so users can set up community and trait-based models with the minimum of R gymnastics. Additionally, most of the methods and functions in the package have default options and assumptions. These can be changed by the user once they are familiar with the models

This vignette starts by summarising the principles and assumptions of size spectrum models. The mizer package is then introduced by showing how to set up the simplest types of size spectrum models: the community and trait-based model. These sections give a basic overview of the classes and methods used by mizer. Simple examples are given that demonstrate how trophic-cascades can be simulated. There then follows a more detailed description of the mizer classes and methods using a multispecies model of the North Sea as an example. Next, there is a detailed example of a multispecies size spectrum model of the North Sea, including running projections using historical fishing patterns. After this, we introduce the scale-invariant trait-based model, which can be thought of as a modified version of the trait-based model that can be organized into a well understood steady state without the need to impose external stock-recruitment relationships. Next we describe how species from the scale-invariant can act as a type of background into which explicit species of particular interest can be added. Finally we describe improvements that have been made to the previous version of mizer, and discuss some technical details in the appendix.

2 Package installation and getting help

2.1 Installing mizer

mizer is a package for the R open-source statistical programming language. R is available from the CRAN website, which is also an excellent source of documentation and tutorials.

The easiest way to install mizer (assuming you have an active internet connection) is to start an R session and then type:

```
install.packages("mizer")
```

After installing mizer, to actually use it you need to load the package using the library() function. Note that whilst you only need to install the package once, it will need to be loaded every time you start a new R session.

```
library(mizer)
```

The source code for mizer is hosted on Github (https://github.com/sizespectrum/mizer). If you are feeling brave and wish to try out a development version of mizer you can install the package from here using the R package devtools (which was used extensively in putting together mizer).

2.2 Getting help

As you probably know, to access documentation in R you can use the help() function. This can be used to access package documentation in a range of ways. For example:

```
help(package="mizer")
help(mizer)
help(project)
```

The first command gives a technical summary of the package, including the available functions. The second command gives a brief introduction to mizer. The third gives the documentation page for the method project().

Some methods are associated with several R classes. For example, the plot() method is generic and can be used on a wide range of R objects. The plot() method has been overloaded in mizer to plot *MizerSim* objects. To select the help page for the appropriate plotting method you can either just use help(plot) and then select from a menu of packages or you can supply the package name in the help() command:

```
help(plot, package="mizer")
```

There are other ways of accessing package documentation that you may not be familiar with. To access the help page of a particular method you can use: method? method-name. For example, to access the help page of the getFeedingLevel() method you can use:

```
method ? getFeedingLevel
```

This also works for getting information on a class. For example, to get the help page on the *Mizer-Params* class you can use:

These two ways of getting help can be useful when a class and a method have the same name. For example, *MizerParams* is a class and also the name of the method for creating *MizerParams* objects.

3 Size spectrum modelling - concepts, processes and assumptions

Size spectrum models have emerged as a conceptually simple way to model a large community of individuals which grow and change trophic level during life. There is now a growing literature describing different types of size spectrum models (e.g. Andersen and Beyer, 2006; Andersen et al., 2008; Benoît and Rochet, 2004; Hartvig, 2011; Hartvig et al., 2011; Law et al., 2009). The models can be used to understand how marine communities are organised (Andersen and Beyer, 2006; Andersen et al., 2009a; Blanchard et al., 2009) and how they respond to fishing (Andersen and Pedersen, 2010; Andersen and Rice, 2010). This section introduces the central assumptions, concepts, processes, equations and parameters of size spectrum models.

Roughly speaking there are three versions of the size spectrum modelling framework of increasing complexity: The *community* size spectrum model (Benoît and Rochet, 2004; Blanchard et al., 2009; Law et al., 2009; Maury et al., 2007), the *trait-based* size spectrum model (Andersen and Beyer, 2006; Andersen and Pedersen, 2010), and the *multispecies* spectrum model (Hartvig et al., 2011). The community and trait-based models can be considered as simplifications of the multispecies model. This section focuses on the multispecies model but is also applicable to the community and trait-based models. mizer is able to implement all three types of model using similar commands.

3.1 Central concepts and assumptions

Size spectrum models are a subset of physiologically structured models (De Roos and Persson, 2001; Metz and Diekmann, 1986) as growth (and thus maturation) is food dependent, and processes are formulated in terms of individual level processes. All parameters in the size spectrum models are related to individual weight which makes it possible to formulate the model with a small set of general parameters (Table 1), which has prompted the label "charmingly simple" to the model framework (Pope et al., 2006).

The model framework builds on two central assumption and a number of lesser standard assumption.

The first central assumption is that an individual can be characterized by its weight w and its species number i only. The aim of the model is to calculate the size- and trait-spectrum $\mathcal{N}_i(w)$ which is the density of individuals such that $\mathcal{N}_i(w)dw$ is the number of individuals in the interval [w:w+dw]. The dimensions of the size spectrum are numbers per weight per volume. Scaling from individual-level processes of growth and mortality to the size spectrum of each trait group is achieved by means of the McKendrik-von Foerster equation, which is simply a conservation equation:

$$\frac{\partial N_i(w)}{\partial t} + \frac{\partial g_i(w)N_i(w)}{\partial w} = -\mu_i(w)N_i(w)$$
(3.1)

where individual growth $g_i(w)$ and mortality $\mu_i(w)$ are both determined by the availability of food from the other species plus a background resource, $N_R(w)$, and predation by the other species. The conservation equation is supplemented by a boundary condition at the boundary at weight w_0 where the flux of individuals (numbers per time) $g_i(w_0)N_i(w_0)$ is determined by the reproduction of offspring by mature individuals in the population R_i :

$$g_i(w_0)N_i(w_0) = R_i. (3.2)$$

The second central assumption is that the preference of food is determined by individual weight combined with a species preference. The preference for prey weight is described by the log-normal selection model (Ursin, 1973) which prescribes prey preference in terms of the ratio between the weight of predators w and prey of weight w_n :

$$\phi_i(w_p/w) = \exp\left[\frac{-(\ln(w/(w_p\beta_i)))^2}{2\sigma_i^2}\right],\tag{3.3}$$

where β_i is the preferred predator-prey mass ratio and σ_i the width of the weight selection function.

The rest of the formulation of the model rests on a number of "standard" assumptions from ecology and fisheries science about how encounters between predators and prey leads to growth $g_i(w)$ and recruitment R_i of the predators, and mortality of the prey $\mu_i(w)$. The remainder of this section looks in detail at these assumptions.

3.2 Predator-prey encounter

The encounter of food is based on the "Andersen-Ursin" encounter model which was developed as part of a North-Sea ecosystem model (see also Andersen and Beyer, 2006; Andersen and Ursin, 1977).

The available food (mass per volume) for a predator of weight w is determined by integrating over all species and the background resource weighted by the size selection function (Equation 3.3):

$$E_{a.i}(w) = \int \left(N_R(w_p) + \sum_j \theta_{ij} N_j(w_p) \right) \phi_i(w_p/w) w_p \, dw_p. \tag{3.4}$$

where θ_{ij} is the preference of species *i* for species *j*. The food actually encountered $E_{e.i}$ (mass per time) depends on the search rate (volume per time) which is assumed to scale with individual weight as $\gamma_i w^q$:

$$E_{e\,i}(w) = \gamma_i w^q E_{a\,i}(w). \tag{3.5}$$

3.3 Consumption

The encountered food is consumed subjected to a standard Holling functional response type II to represent satiation. This determines the feeding level, $f_i(w)$, which is a dimensionless number between 0 (no food) and 1 (fully satiated) so that $1 - f_i(w)$ is the proportion of the encountered food that is consumed. It is given by

$$f_i(w) = \frac{E_{e.i}(w)}{E_{e.i}(w) + h_i w^n},$$
(3.6)

where $h_i w^n$ is the maximum consumption rate. The rate at which food is consumed is then $(1 - f_i(w))E_{e,i}(w) = f_i(w)h_i w^n$.

3.4 Growth

The consumed food is assimilated with an efficiency α and used to fuel the needs for standard metabolism (at a rate $k_{s.i}w^p$) and activity and movement (at a rate k_iw). The remaining rate, if any,

$$E_{r,i}(w) = \max(0, \alpha f_i(w) h_i w^n - k_{s,i} w^p - k_i w)$$
(3.7)

is used for growth and reproduction. When food supply does not cover the requirements of metabolism and activity, growth and reproduction stops, i.e. there is no negative growth².

The proportion of $E_{r,i}(w)$ that is used for reproduction is given by a function $\psi_i(w)$ that changes between zero around the weight of maturation $w_{m,i}$ to one at the asymptotic weight W_i where all available energy is used for reproduction:

$$\psi_i(w) = \left[1 + \left(\frac{w}{w_{m.i}}\right)^{-u}\right]^{-1} \left(\frac{w}{W_i}\right)^{1-n},\tag{3.8}$$

The default value of u is 10. The term in the square bracket is a function that varies smoothly from 0 to 1 around the weight at maturation. The last term describes how the relative amount of energy invested in reproduction increases as the weight approaches the asymptotic weight.

Thus the somatic growth function is given by

$$g_i(w) = E_{r,i}(w) (1 - \psi_i(w)).$$
 (3.9)

The form of the allocation function (3.8) is chosen such that the growth curve approximates a von Bertalanffy growth curve if the feeding level is constant (see Figure 1 and Hartvig et al. (2011) for details about the derivation). The actual emerging growth curves from the model will depend on the feeding level, and may even result in stunted growth curves if the feeding level drops below the *critical feeding level* where the assimilated food is just enough to satisfy standard metabolism:

$$f_{c.i}(w) = \frac{k_{s.i}w^p + k_iw}{\alpha h_i w^n}.$$
(3.10)

If n = p and k = 0 (which is the case for the set of default parameters chosen here), f_c is independent of w.

3.5 Reproduction

The total production rate of eggs $R_{p,i}$ (numbers per time) is found by integrating the contribution from all individuals:

$$R_{p.i} = \frac{\epsilon}{2w_0} \int N_i(w) E_{r.i}(w) \psi_i(w) dw, \qquad (3.11)$$

where the individual contribution is obtained by multiplying the rate at which the individual allocates energy to reproduction by an efficiency factor ϵ and then dividing by the egg weight w_0 to convert the energy into number of eggs. The result is multiplied by a factor 1/2 to take into account that only females reproduce.

3.6 Recruitment

One of the fundamental assumptions in fisheries science is that marine fish populations experience significant density dependence early in life (Ricker, 1954). This assumption has some empirical backing

² The individual would then be subjected to a starvation mortality. Starvation is usually not an important process in the multispecies model with Beverton-Holt recruitment. It is therefore not implemented in mizer at the moment.

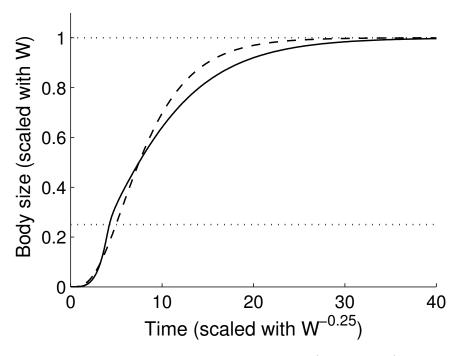


Figure 1: The growth curve of an individual found by solving (Equation 3.9) with a constant feeding level $f_0 = 0.6$ (solid line), compared to a von Bertalanffy growth curve with the von Bertalanffy growth parameter $K = (\alpha f_0 h w^n - k_s w^n) W^{n-1}/3$ (dashed line) (Andersen et al., 2009b).

for selected, well-studied stocks (Myers and Cadigan, 1993) and is also supported by the general observation that marine fish do not experience strong, food-dependent growth. This is in contrast to fish in lakes where stunted growth is not uncommon. From a technical point of view, additional density dependence is needed to stabilize the model community to avoid some of the trait classes going extinct (Hartvig, 2011). An alternative way to ensure coexistence of many species is to introduce a random food web matrix describing species-specific food preference (Hartvig et al., 2011) or an abstract notion of space (Hartvig, 2011).

In mizer, density dependence is modelled as a compensation on the egg production. This can be considered as the stock-recruitment relationship (SRR). The default functional form is such that the recruitment flux R_i (numbers per time) approaches a maximum recruitment as the egg production increases, modelled mathematically analogous to the Holling type II function response as a "Beverton-Holt" type of SRR:

$$R_i = R_{\max.i} \frac{R_{p.i}}{R_{p.i} + R_{\max.i}},$$
(3.12)

where $R_{\max.i}$ is the maximum recruitment flux of each trait class (Figure 2).

The "Beverton-Holt" type of SRR is not the only density dependence model that mizer can use. Users are able to write their own model so it is possible to set a range of SRRs, e.g. fixed recruitment (as used in the community-type model) or "hockey-stick". This is explored in more detail in Section 8.4.

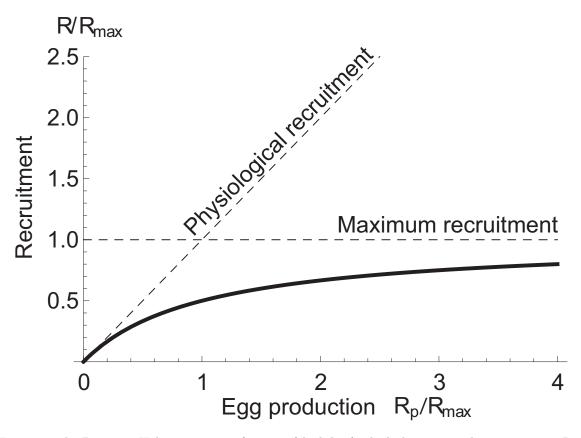


Figure 2: The Beverton-Holt recruitment function (thick line) which determines the recruitment R as a function of the egg production (the "physiological recruitment") R_p via (Equation 3.12).

3.7 Mortality

The mortality rate of an individual $\mu_i(w)$ has three sources: predation mortality $\mu_{p.i}(w)$, background mortality $\mu_{b.i}(w)$ and fishing mortality $\mu_{f.i}(w)$.

Predation mortality is calculated such that all that is eaten translates into corresponding predation mortalities on the ingested prey individuals. Recalling that $1 - f_j(w)$ is the proportion of the food encountered by a predator of species j and weight w that is actually consumed, this gives:

$$\mu_{p,i}(w_p) = \sum_{j} \theta_{ji} \int \phi_j(w_p/w) (1 - f_j(w)) \gamma_j w^q N_j(w) dw$$
 (3.13)

(see Hartvig et al. (2011, Appendix A) for derivation)

Background mortality $\mu_{b.i}(w)$ can be set freely in mizer. By default it is assumed to be constant within a species and inversely proportional to generation time (Peters, 1986):

$$\mu_{b.i} = \mu_0 W_i^{n-1}. \tag{3.14}$$

The background mortality is needed to ensure that the largest individuals in the community also experience mortality as they are not predated upon by any individuals from the community spectrum. Fishing mortality $\mu_{f,i}(w)$ is discussed further in section 8.3.

3.8 Resource dynamics

The background resource spectrum $N_R(w)$ represents food items for the smallest individuals (smaller than βw_0). The temporal evolution of each size group in the resource spectrum is described using semi-chemostatic growth:

$$\frac{\partial N_R(w,t)}{\partial t} = r_0 w^{p-1} \left[c_p(w) - N_R(w,t) \right] - \mu_p(w) N_R(w,t), \tag{3.15}$$

where $r_0 w^{p-1}$ is the population regeneration rate (Fenchel, 1974; Savage et al., 2004) and $c_p(w)$ is the carrying capacity, which takes the value $\kappa w^{-\lambda} = \kappa w^{-2-q+n}$ by default. The predation mortality rate is given by a similar expression as in (3.13):

$$\mu_p(w_p) = \sum_j \int \phi_j(w_p/w)(1 - f_j(w))\gamma_j w^q N_j(w) dw.$$
 (3.16)

3.9 Parameters

The default parameter values for the model have been derived on the basis of meta-analyses of data on marine fish (Table 1). Two parameters deserving special mention are the initial and critical feeding levels. These are used as physiological measures characterizing the productivity of the system and the metabolic requirements of the individuals.

The system is driven by the production of the resource. The ratio between the production and the maximum consumption will determine the feeding level f_0 of small individuals feeding mainly on the background resource. If f_0 is close to 1 the individuals are satiated, and growth will be largely independent of changes in food availability. If f_0 is in the linear range of the functional response, growth will be dependent on available food. If f_0 is close to the critical feeding level f_c , where the available food is only sufficient to cover standard metabolism, growth will be stunted. The initial feeding level f_0 , calculated as the feeding level of an individual feeding on the resource at carrying capacity, is used as the control parameter for the resource productivity. The initial feeding level is then used to calculate the search rate parameter γ , see (Andersen and Beyer, 2006, Appendix B):

$$\gamma_i(f_0) = \frac{f_0 h_i \beta_i^{2-\lambda} \exp(-(\lambda - 2)^2 \sigma_i^2 / 2)}{(1 - f_0) \sqrt{2\pi} \kappa \sigma_i}.$$
 (3.17)

Similar to the way the initial feeding level f_0 is used to describe the relation between the production and the maximum consumption, the critical feeding level f_c (Equation 3.10) is used to describe the relation between the factors for standard metabolism k_s and maximum consumption h. A critical feeding level of $f_c \approx 0.2$ seems to be reasonable (Hartvig et al., 2011).

The free parameter κ may in principle be determined analytically, based on an assumption that all species have maximum recruitment, $R_i = R_{\max,i}$. However, the depletion of resources makes it difficult to find an analytical approximation of κ and until that has been achieved, κ has to be adjusted manually such that the resulting community spectrum forms a continuation of the resource spectrum.

4 Introducing mizer

With mizer is is possible to implement the three types of model mentioned above (with increasing complexity): community, trait-based and multispecies, using the same basic tools and methods. For the remainder of this vignette we present examples of how to set up, project and analyse all three types of model.

Using the package is relatively simple. There are three main stages to implementing a model:

- Setting the model parameters. This is done by creating an object of class *MizerParams*. This includes model parameters such as the life history parameters of each species, and the fishing gears. It is possible to create a *MizerParams* object directly using the class constructor or by using one of the convenient wrapper functions provided in the package.
- Running a simulation. This is done by calling the project() method on the model parameters. This produces an object of *MizerSim* which contains the results of the simulation. The project() method controls the length and time-step of the simulation, as well as the levels of fishing effort.
- Exploring the results. After a simulation has been run, the results can be examined using a range of plots and summaries.

These stages and the accompanying classes and methods are explained in detail in the rest of the document.

It is probably easier to learn the basics of mizer through examples. We do this by looking at three set-ups of the framework: the community model, the trait-based model and the multi-species model. The three types of model represents a hierarchy of complexity: the community model is the simplest and the multi-species model the most complex. The common denominator is the reliance of a size-based description of the structure of the fish community and of the predator-prey interactions between individuals.

In the community model, individuals are only characterized by their size and are represented by a single group representing an across species average. Community size spectrum models have been used to investigate how abundance size spectra emerge solely from individual-level process of size-based predation and how fishing impacts metrics of community-level size spectra (Benoît and Rochet, 2004; Law et al., 2009). Since few parameters are required it has been used for investigating large-scale community-level questions where detailed trait- and species-level parameterisations are not tractable (Barange et al., 2014).

The trait-based model resolves a continuum of species with varying asymptotic sizes. The asymptotic size, W_{∞} , is considered to be the most important trait that characterizes the species life history. The continuum is represented by a discrete number of species spread evenly over the range of asymptotic sizes. The number of species is not important and does not affect the general dynamics of the model (Andersen and Pedersen, 2010). Many of the parameters, such as β and σ , are the same for all species. Other model parameters are determined by the asymptotic size. For example, the weight at maturation is given by, $W_{mat} = \eta_m W_{\infty}$, where the default value of η_m is 0.25. In the trait-based model species-level complexity is captured through different life histories, and both intra- and inter-specific size spectra emerge (Andersen and Beyer, 2006; Andersen and Pedersen, 2010). This approach is powerful for examining the generic population and whole community level responses to both size and species selective fishing without the requirement for detailed species-specific parameters (Andersen and Rice, 2010; Jacobsen et al., 2014).

In the multispecies model individual species are resolved in detail and each has distinct life history, feeding and reproduction parameters. More detailed information is required to parameterise the multispecies model but the approach can be used to address management strategies for a realistic community in a specific region or subset of interacting species (Blanchard et al., 2014).

All three models predict abundance, biomass and yield as well as predation and mortality rates at size. They are useful for establishing baselines of abundance of unexploited communities, for understanding how fishing impacts aquatic communities and for testing indicators that are being developed to support an ecosystem approach to fisheries management. Which model to use in a specific case depends on needs and on the amount of information available to calibrate the model. The multi-species model

could be set up for most systems where calibration parameters can be estimated. This requires a lot of insight and data. If the parameters are just guesstimates the results of the multi-species model will be no more accurate than the results from the trait-based model. In such situations we therefore recommend the use of the trait-based model, even though it only provides general information about the asymptotic size distribution and not about specific species. The community model is useful for large-scale community-level questions where only the average spectrum is needed. Care should be taken when the community model is used to infer the dynamical properties of marine ecosystems, since it is prone to unrealistically strong oscillations due to the lack of dampening effects provided by the life-history diversity in the trait-based and multi-species models (Zhang et al., 2013).

5 Implementing a community-type model

5.1 Introduction

The simplest version of the size spectrum model is the community model, originally introduced by (Benoît and Rochet, 2004). In this model only one "species" is resolved. Reproduction is not considered, so $\psi(w) = 0$ and the recruitment flux R is set to be constant. The resource spectrum only extends to the start of the community spectrum. Standard metabolism is turned off by setting k_s to 0. Growth is therefore given by the simpler equation:

$$g(w) = \alpha f(w)hw^n \tag{5.1}$$

where $f(w)hw^n$ is the consumed food and α is the efficiency with which the consumed food is transformed into growth. The growth rate can also be written as:

$$q(w) = \bar{\epsilon}_I E_a \tag{5.2}$$

where $\bar{\epsilon}_I$ is the average growth efficiency which can be derived from the full model (see Andersen et al., 2009a; Zhang et al., 2013).

In this section we describe how a community model can be set up and projected through time. We then use a community model to illustrate the idea of a 'trophic cascade'. Due to the relative simplicity of this type of model they are useful for gently introducing some of the concepts behind the mizer package. Consequently, this section should hopefully serve as an introduction to using mizer and some of the main classes and methods.

5.2 Setting up a community model

As mentioned above, the first stage in implementing a model using mizer is to create an object of class *MizerParams*. This class contains the model parameters including the life-history parameters of the species in the model, the stock-recruitment relationships, the fishing selectivity functions and the parameters of the resource spectrum. The class is fully described in Section 8.

To avoid having to make a *MizerParams* object directly, a wrapper function, set_community_model(), has been provided that conveniently creates a *MizerParams* object specifically for a community model. The documentation for the function can be seen by entering:

?set_community_model

As can be seen in the help page, the function can take many arguments. These are passed on to the *MizerParams* constructor when the function is called. We can ignore most of these arguments for the

moment as they almost all come with default values. Full details of those arguments can be seen in Section 8.

The arguments that you should pay attention to are: z0 (the level of background mortality), alpha (the assimilation efficiency of the community), f0 (the average feeding level of the community which is used to calculate γ in Equation 3.17) and recruitment (the level of constant recruitment).

Although default values for these parameters are provided, you are encouraged to explore how changing the values affects the simulated community. For example, the default value of z0 is 0.1. Increasing this value effectively 'shortens' the length of the community spectrum. The value of the constant recruitment should be set so that the community spectrum is a continuation of the background spectrum. This can be done with trial and error. A reasonable value for alpha is 0.2 (Andersen et al., 2008).

The set_community_model() function is called by passing in the arguments by name. Any parameter that is not passed in is set to the default value. For example, the following line sets up the parameters with z0 = 1, f0 = 0.7, alpha = 0.2 and recruitment = 4e7. All other parameters will have their default value:

```
params <- set_community_model(z0 = 0.1, f0 = 0.7, alpha = 0.2, recruitment = 4e7)
```

Calling the function creates and returns an object of type *MizerParams*. We can check this using the class() function.

```
class(params)

## [1] "MizerParams"

## attr(,"package")

## [1] "mizer"
```

If you are going through this vignette for the first time, it is likely that you have no idea what a *MizerParams* object actually is. In "R-speak" it is an S4 object, which means it is an object made up of "slots". Slots are essentially containers that store the object data. The names of these slots can be seen by calling the slotNames() method on the object:

```
slotNames(params)
    [1] "w"
                             "dw"
##
                                                  "w_full"
##
    [4] "dw_full"
                             "psi"
                                                  "initial_n"
    [7] "intake_max"
                             "search_vol"
                                                  "activity"
## [10] "std_metab"
                             "ft_pred_kernel_e"
                                                 "ft_pred_kernel_p"
##
  [13]
        "mu_b"
                             "rr_pp"
                                                  "cc_pp"
##
  [16]
        "sc"
                             "initial_n_pp"
                                                  "species_params"
  [19] "interaction"
                             "srr"
                                                  "selectivity"
                             "n"
                                                  "p"
   [22]
        "catchability"
##
                                                  "f0"
   [25]
        "lambda"
                             "q"
##
##
  [28] "kappa"
                             "A"
                                                  "linecolour"
## [31] "linetype"
```

As you can see, the params object is made up of lots of slots. They are discussed in detail in Section 8. A quick description can be found in the *MizerParams* help page (run class? MizerParams. The slots of an object are accessed by using the @ operator. For example, to access the w slot (which contains a vector of the size bins in the model) you would use:

```
params@w
```

Rather than picking through the slots to find out what is in a particular *MizerParams* object, a summary of the object can be seen by calling the summary() method on it:

```
summary(params)
## An object of class "MizerParams"
## Community size spectrum:
  minimum size: 0.001
##
   maximum size: 1e+06
##
  no. size bins: 100
## Background size spectrum:
##
   minimum size: 1e-10
##
   maximum size: 1e+06
  no. size bins: 177
## Species details:
##
               species w_inf w_mat beta sigma
## Community Community 9e+05
                               NA 100
## Fishing gear details:
   Gear Target species
##
     Community Community
```

In the summary you can see that the size range of the community spectrum has been set from 0.001 to 10^6 and these are spread over 100 size bins. Similar information is available for the background resource spectrum. Additionally, the community is made up of only one species, called "Community", which has an asymptotic size of 9×10^5 and a preferred predator prey mass ratio of 100. The w_mat parameter has been set to NA as it is not used when running a community model. These values have all been set by default using the set_community_model() function. If you want to set different values for these, you will need to call the set_community_model() function and pass in the the desired argument values.

5.3 Running the community model

By using the set_community_model() method we now have a MizerParams object that contains all the information we need about the model community. We can use this to perform a simulation and project the community through time. In the mizer package, projections are performed using the project() method. You can see the help page for project() for more details and it is described fully in Section 9. We will ignore the details for the moment and just use project() to run some simple projections. The arguments for project() that we need to be concerned with are effort, which determines the fishing effort (and therefore fishing mortality) through time, and t_max, which is the length of the simulation. Initial population abundances are set automatically by the get_initial_n() function. It is possible to set your own initial abundances but we will not do this here.

To run a projection for 50 time steps, with no fishing effort (i.e. we want to model an unexploited community) we run:

```
sim <- project(params, t_max=50, effort = 0)</pre>
```

The resulting object, sim, is of type MizerSim. This class holds the results of the simulation, including the community and background resource abundances at size through time, as well as the original model parameters. It is explained in detail in Section 9.

After running the projection, it is possible to explore the results using a range of plots and analyses. These are described fully in Section 10. To quickly look at the results of the projection you can call the generic plot() method. This plots the feeding level, predation mortality, fishing mortality and abundance by size in the last time step of the simulation, and the biomass through time (Figure 3) Each of the plots can be show individually if desired.

plot(sim)

In Figure 3 there are several things going on that are worth talking about. Looking at the total biomass of the community against time, you can see that the biomass quickly reaches a stable equilibrium. The other panels show what is happening at the last time step in the simulation, which in this case is when the community is at equilibrium. Fishing mortality is 0 because we set the effort argument to 0 when running the simulation. The predation mortality rate (M2) is clearly a function of size, with the smallest sizes experiencing the highest levels of predation. The feeding level describes how satiated an individual is, with 0 being unfed, and 1 being full satiated. The feeding level at size will be strongly affected by the values of the f0 and alpha arguments passed to the set_community_model() function. The background resource and community spectra are shown in the bottom panel of the plot (the plotted background resource spectrum has been truncated to make for a better plot, but really extends all the way back to 10^{-10} g). You can see that the community spectrum forms a continuum with the resource spectrum. This is strongly affected by the level of fixed recruitment (the recruitment argument passed to set_community_model()).

Note the "hump" in the biomass at the largest end of the community spectrum. This is because the size spectrum model can be broadly described as 'big things eating little things'. Given this, what is eating the very biggest things? Without fishing pressure, the mortality of the largest individuals is only from the background mortality (determined by the z0 argument) and the mortality from predation is almost 0. This is difficult to see in the plot due to the M2 being so high for the smaller individuals.

We can see this more clearly by extracting the predation mortality information from the *MizerSim* object, sim, that we created above. This is easily done by using the getM2() method (see the help page for more details). There are several methods that can be used for extracting information from a *MizerSim* object, e.g. getFeedingLevel() and getFMort(). For more information see Section 10. Here we just call getM2() using the sim object:

m2 <- getM2(sim)

This m2 object is a array that contains the predation mortality at time by species by size. Here we only have one species so the species dimension is dropped, leaving us with a two dimensional array of time by size. We projected the model for 50 time steps but the length of the time dimension is 51 as the initial population is also included as a time step.

To pull out the predation mortality at size in the final time step we use:

m2[51,]

If you plot this predation mortality on a log-log scale you can see how the predation mortality declines to almost zero for the largest sizes (Figure 4).

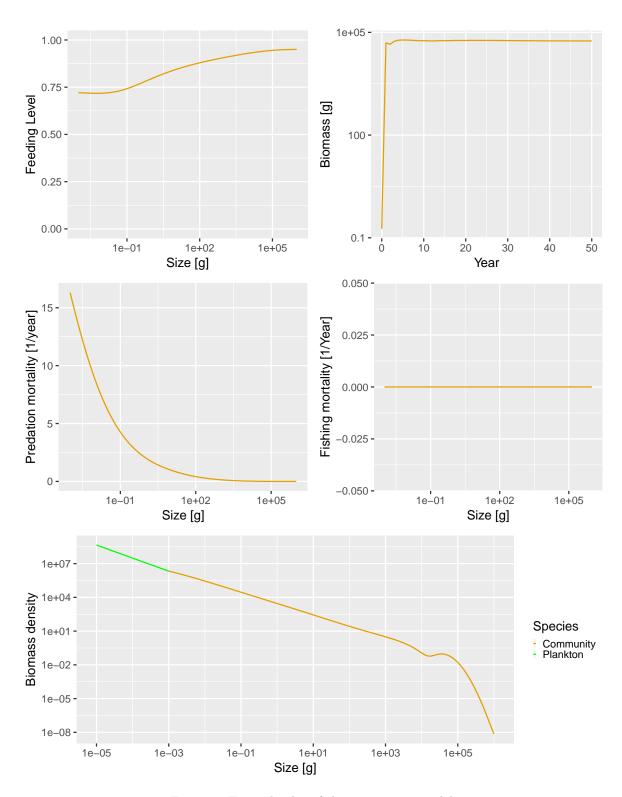


Figure 3: Example plot of the community model.

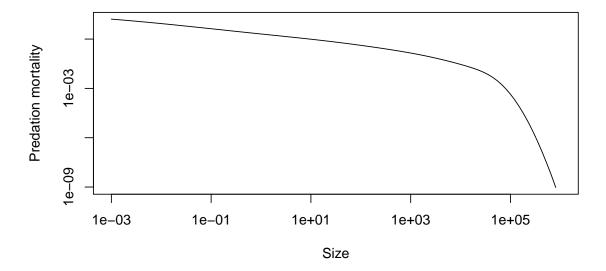


Figure 4: Predation mortality without fishing in the community model (note the log scales for both axes).

5.4 Example of a trophic cascade with the community model

It is possible to use the community model to simulate a trophic cascade, similar to those seen in Andersen and Pedersen (2010). To do this we need to perform two simulations, one with fishing and one without.

This means we need to consider how fishing is handled in mizer. The set_community_model() function automatically sets the fishing selectivity to have a knife-edge shape, with only individuals larger than 1 kg selected (the size at the knife-edge can be changed by setting the knife_edge_size argument). Although it is possible to change the selectivity function, here we will use the default knife-edge selectivity. Here we set up the parameter object exactly as before, but now we are explicitly setting the size at which individuals are selected by the fishing gear.

```
params_knife <- set_community_model(z0 = 0.1, recruitment = 4e7,
    alpha = 0.2, f0 = 0.7, knife_edge_size = 1000)</pre>
```

First we perform a simulation without fishing in the same way we did above by setting the effort argument to 0:

```
sim0 <- project(params_knife, effort = 0, t_max = 50)</pre>
```

Now we want to simulate again, this time with fishing. In the simulations, fishing mortality is calculated as the product of the fishing selectivity, effort and catchability (see Section 8.3 for more details). By default catchability is set to 1. This means that a fishing effort of 1 will result in a fishing mortality of 1 for fully selected sizes. Here we run a simulation with fishing effort set to 1 for the duration of the simulation:

```
sim1 <- project(params_knife, effort = 1, t_max = 50)</pre>
```

You can compare the difference between these scenarios by using the plot() method as before (Figure 5). Of particular interest is the fishing mortality at size. The knife-edge selectivity at 1000 g can be clearly seen and an effort of 1 has resulted in a fishing mortality of 1 for the fully selected sizes.

```
plot(sim1)
```

To explore the presence of a trophic cascade, we are interested in looking at the relative change in abundance when the community is fished compared to when it is not fished. To do this we need to get the abundances at size from the simulation objects. The abundances are store in the n slot of the MizerSim objects. The n slot contains a three dimensional array with dimensions time n species n size. Here we have 51 time steps (50 from the simulation plus one which stores the initial population), 1 species and 100 sizes:

```
dim(sim0@n)
## [1] 51 1 100
```

We want the abundances in the final time step, and we can use these to calculate the relative abundances:

```
relative_abundance <- sim1@n[51,,] / sim0@n[51,,]
```

This can then be plotted (Figure 6) using basic R plotting commands. The sizes are stored in the params@w slot (a slot of a slot!).

The impact of fishing on species larger than 1000g can be clearly seen. As described in (Andersen and Pedersen, 2010), the fishing pressure lowers the abundance of large fish (the decrease in relative abundance at 1000 g). This then relieves the predation pressure on their smaller prey (the preferred predator-prey size ratio is given by the β parameter, which is set to 100 by default), leading to an increase in their abundance. This in turn increases the predation mortality on their smaller prey, which reduces their abundance and so on.

5.5 The impact of changing σ

As described above, the σ parameter determines the width of the predator prey size preference. Here we take a look at how changing the value of σ can affect the dynamics of the community. In the examples above, σ is set in the set_community_model() function by default to a value of 2. When projected through time, the community abundances converge to a stable equilibrium. What happens if we reduce the value of σ , for example by setting it to 1.0? We can do this by passing in the new value of σ into set_community_model().

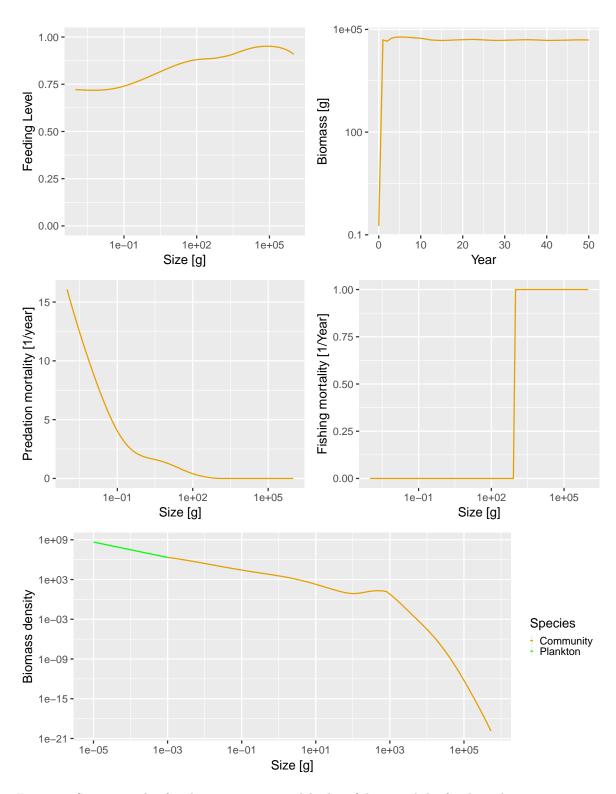


Figure 5: Summary plot for the community model when fishing with knife-edge selectivity at size = 1000 g.

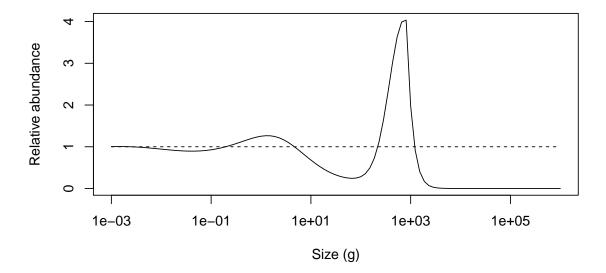


Figure 6: Relative abundances from the unfished (dashed line) and fished (solid line) community model.

We want to project this new model through time using the project() method. Note that we have introduced a new argument: dt. This is the step size of the solver. It does not have anything to do with the biology in the model. It only affects the internal engine of project() that performs the projection. As you can see in the underlying model equations in Section 3, the model runs in continuous time. Therefore, to project it forward, project() must solve the system of equations using numerical methods. The quality of these methods is strongly affected by dt. The default value of dt is 0.1, which will be fine for most of the projections we run in this Vignette. Here it is necessary to reduce the value to 0.01 to avoid introducing any artefacts into the projected values. Decreasing dt increases the time it takes to run a projection. Here we project the new parameters object for 50 time steps without fishing:

```
sim_sigma1 <- project(params_sigma1, effort = 0, t_max = 50, dt=0.01)
```

Let's take a look at how the abundances change through time. We can do this with the plotBiomass() method:

```
plotBiomass(sim_sigma1)
```

Figure 7 shows that abundances of the community no longer converge to a stable equilibrium and the dynamics appear to be chaotic. The ecological significance of the change in dynamics, and of the ability of simple community models to show chaotic behaviour, is still being debated. It can be argued that the size of the oscillations are too large to be 'true'. Additionally, when a trait-based model (see Section 6) is implemented, the magnitude of the oscillations are much smaller.

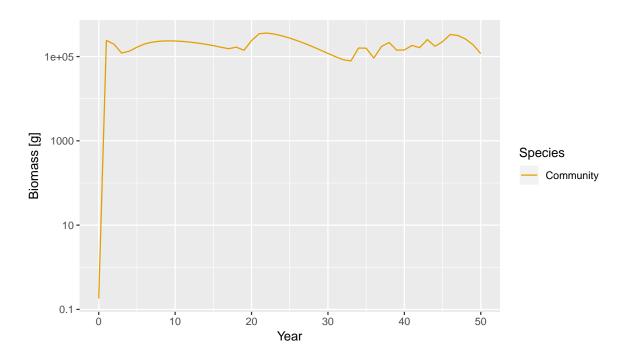


Figure 7: Biomass of the community model when σ is reduced to a value of 1.0.

6 Implementing a trait-based model

6.1 Introduction

As mentioned above, the trait-based size spectrum model can be derived as a simplification of the general model outline in Section 3. It is more complicated than a community model and the most significant difference between the two is that while the community model only resolves a single "species", the trait-based model resolves many species. In a trait-based model the asymptotic size is considered to be the most important "trait" characterizing a species. All of the species-specific parameters, such as β and σ , are the same for all species. Other model parameters are determined by the asymptotic size. For example, the weight at maturation, $w_m = \eta_m W$, where $\eta_m = 0.25$. The number of species is not important and does not affect the general dynamics of the model. The asymptotic sizes of the species are spread evenly over the size range of the community. For applications of the trait-based model see Andersen and Pedersen (2010) and Andersen and Rice (2010).

6.2 Setting up a trait-based model

To help set up a trait-based model, there is a wrapper function, set_trait_model(). Like the set_community_model() function described above, this function can take many arguments. Most of them have default values so you don't need to worry about them for the moment. See the help page for more details.

?set_trait_model

The main parameters of interest are the number of the species in the model (no_sp) and the minimum

and maximum asymptotic sizes (min_w_inf and max_w_inf respectively, the asymptotic sizes are spread evenly on a logarithmic scale).

One of the key differences between the community type model described above and the trait-based model is that reproduction and egg production are considered. In the community model, recruitment is constant and there is no relationship between the abundance in the community and egg production. In the trait-based model, the egg production is modeled using a "Beverton-Holt" type function (the default in mizer, see Section 3.6) where the recruitment flux R_i (numbers per time) approaches a maximum recruitment as the egg production increases. The maximum recruitment flux is calculated using equilibrium theory (see Andersen and Pedersen, 2010) and a recruitment multiplier k_0 , which can be passed in as an argument (k0) to the set_trait_model() function. k0 has a default value of 50.

Here we set up the model to have 10 species, with asymptotic sizes ranging from 10 g to 100 kg. All the other parameters have default values.

```
params <- set_trait_model(no_sp = 10, min_w_inf = 10, max_w_inf = 1e5)</pre>
```

This function returns an object of type *MizerParams*, which holds all the model information, including species parameters.

```
class(params)

## [1] "MizerParams"

## attr(,"package")

## [1] "mizer"
```

This object can therefore be interrogated in the same way as described in Section 5 above, either by inspecting the individual slots or by using the summary() function.

```
summary(params)
## An object of class "MizerParams"
## Community size spectrum:
  minimum size: 0.001
##
##
   maximum size: 110000
  no. size bins: 100
## Background size spectrum:
##
   minimum size: 1.03406e-10
##
   maximum size: 110000
  no. size bins: 186
## Species details:
##
     species
                    w_inf
                                 w_mat beta sigma
## 1
           1
                10.00000
                              2.500000 100
                                              1.3
## 2
           2
                 27.82559
                              6.956399 100
## 3
           3
                 77.42637
                             19.356592 100
                                              1.3
           4
                215.44347
                             53.860867
                                        100
## 4
                                              1.3
                            149.871063 100
## 5
           5
                599.48425
                                              1.3
## 6
           6
              1668.10054
                            417.025134
                                        100
                                              1.3
## 7
           7
               4641.58883
                           1160.397208
                                        100
                                              1.3
      8 12915.49665 3228.874163
## 8
                                        100
                                              1.3
```

```
## 9     9     35938.13664    8984.534160    100     1.3
## 10     10 100000.00000    25000.000000    100     1.3
## Fishing gear details:
## Gear Target species
## knife_edge_gear    1 2 3 4 5 6 7 8 9 10
```

The summary shows us that now we have 10 species in the model, with asymptotic sizes ranging from 10 to 10^5 . The size at maturity (w_mat) is linearly related to the asymptotic size. Each species has the same preferred predator-prey mass ratio parameter values (beta and sigma, see Equation 3.3). There are 100 size bins in the community and 186 size bins including the background resource spectrum. Ignore the summary section on fishing gear for the moment. This is explained later.

6.3 Running the trait-based model

As with the community model described above, we can project the model through time using the project() method. Here we project the model for 75 time steps and without any fishing (the effort argument is set to 0). We use the default initial population abundances given by the get_initial_n() function so there is no need to pass in any initial population values (see Section 9.3).

```
sim <- project(params, t_max=75, effort = 0)</pre>
```

This results in a *MizerSim* object which contains the abundances of the community and background resource spectra through time, as well as the original *MizerParams* object. As with the community model, we can get a quick overview of the results of the simulation by calling the generic plot() method:

```
plot(sim)
```

The summary plot has the same panels as the one generated by the community model, but here you can see that all the species in the community are plotted (Figure 8). The panels show the situation in the final time step of the simulation, apart from the biomass through time plot. As this is a trait-based model where all species fully interact with each other, the predation mortality (M2) and feeding level by size is the same for each species. The biomasses quickly settle down to equilibria. In this simulation we turned fishing off so the fishing mortality is 0. The size-spectra show the abundances at size to be evenly spaced by asymptotic size.

6.4 Example of a trophic cascade with the trait-based model

As with the community model, it is possible to use the trait-based model to simulate a trophic cascade, similar to those seen in Andersen and Pedersen (2010). Again, we perform two simulations, one with fishing and one without. We therefore need to consider how fishing gears and selectivity have been set up by the set_trait_model() function.

The default fishing selectivity function is a knife-edge function, which only selects individuals larger than 1000 g. There is also only one fishing gear in operation, and this selects all of the species. You can see this if you call the summary() method on the *params* argument we set up above. At the bottom of the summary there is a section on "Fishing gear details". You can see that there is only one gear, called "knife_edge_gear" and that it selects species 1 to 10. To control the size at which individuals are selected there is a knife_edge_size argument to the set_trait_model() function. This has a default value of 1000 g.

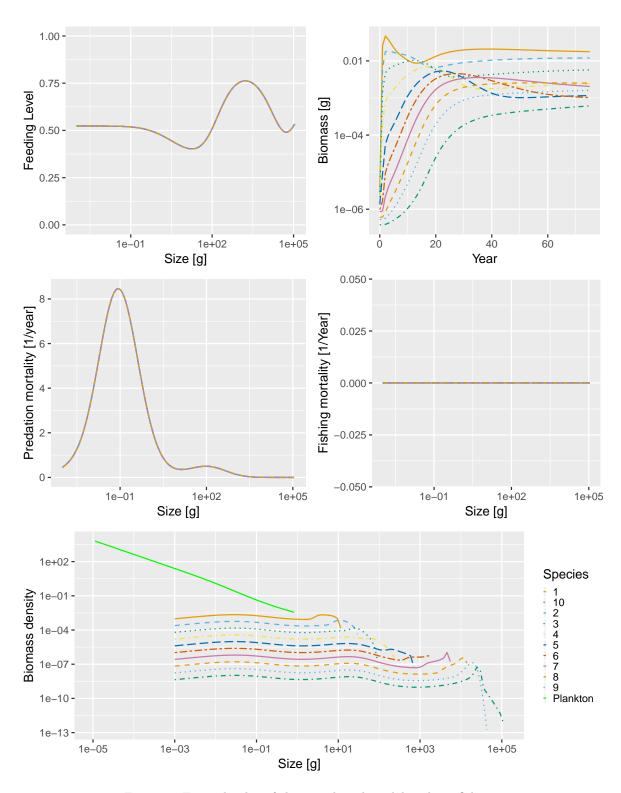


Figure 8: Example plot of the trait-based model with no fishing.

In mizer it is possible to include more than one fishing gear in the model and for different species to be caught by different gears. We will ignore this for now, but will explore it further below when we introduce an industrial fishery to the trait-based model.

To set up the trait-based model to have fishing we set up the *MizerParams* object in exactly the same way as we did before but here the knife_edge_size argument is explicitly passed in for clarity:

First we perform a simulation without fishing in the same way we did above by setting the effort argument to 0:

```
sim0 <- project(params_knife, effort = 0, t_max = 75)</pre>
```

Now we simulate with fishing. Here, we use an effort of 0.75. As mentioned in Section 5.4, the fishing mortality on a species is calculated as the product of effort, catchability and selectivity (see Section 8.3 for more details). Selectivity ranges between 0 (not selected) and 1 (fully selected). The default value of catchability is 1. Therefore, in this simulation the fishing mortality of a fully selected individual is simply equal to the effort. This effort is constant throughout the duration of the simulation (however, this is does not necessarily have to be the case, see Section9).

```
sim1 <- project(params_knife, effort = 0.75, t_max = 75)</pre>
```

Again, we can plot the summary of the fished community using the default plot() function (Figure 9). The knife-edge selectivity at 1000 g can be clearly seen in the fishing mortality panel:

```
plot(sim1)
```

The trophic cascade can be explored by comparing the total abundances of all species at size when the community is fished and unfished. As mentioned above, the abundances are stored in the n slot of the MizerSim object. The n slot returns a three dimensional array with dimensions time x species x size. Here we have 76 time steps (75 from the simulation plus one which stores the initial population), 10 species and 100 sizes:

```
dim(sim0@n)
## [1] 76 10 100
```

As with the community model, we are interested in the relative total abundances by size in the final time step so we want to pull out the 76th time step from the abundances and sum over the species. We can use the apply() function to help us:

```
total_abund0 <- apply(sim0@n[76,,],2,sum)
total_abund1 <- apply(sim1@n[76,,],2,sum)</pre>
```

We can then use these vectors to calculate the relative abundances:

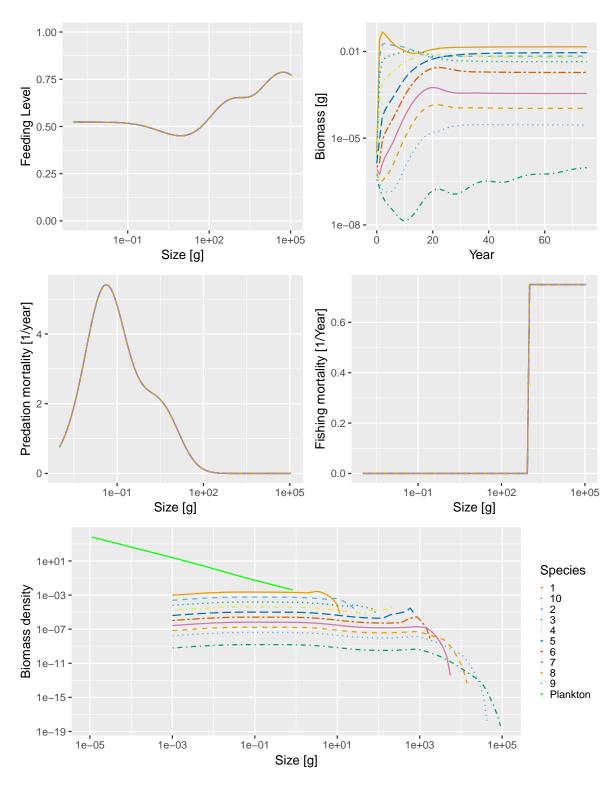


Figure 9: Summary plot for the trait-based model when fishing with knife-edge selectivity at size = 1000 g.

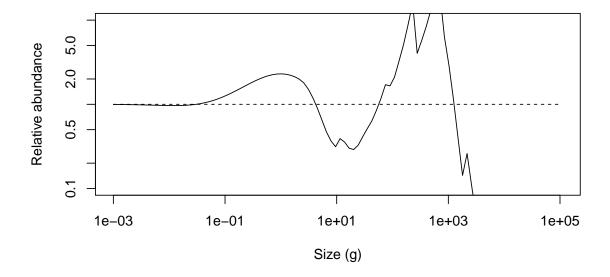


Figure 10: Relative abundances from the unfished (dashed line) and fished (solid line) trait based model.

```
relative_abundance <- total_abund1 / total_abund0
```

Which can be plotted using (Figure 10):

```
plot(x=sim0@params@w, y=relative_abundance, log="xy", type="n", xlab = "Size (g)",
    ylab="Relative abundance", ylim = c(0.1,10))
lines(x=sim0@params@w, y=relative_abundance)
lines(x=c(min(sim0@params@w),max(sim0@params@w)), y=c(1,1),lty=2)
```

The impact of fishing on species larger than 1000 g can be clearly seen. As described above and in (Andersen and Pedersen, 2010), the fishing pressure lowers the abundance of large fish (> 1000 g). This then relieves the predation pressure on their smaller prey (the preferred predator-prey size ratio is given by the β parameter, which is set to 100 by default), leading to an increase in their abundance. This in turn increases the predation mortality on their smaller prey, which reduces their abundance and so on.

This impact can also be seen by looking at the predation mortality by size. The predation mortalities are retrieved using the getM2() method for *MizerSim* objects. This returns a three dimensional array of predation mortalities by time x species x size (see the help page for getM2() for more details). As mentioned above, for the trait based model the predation mortality by size is the same for each species. Therefore we only look at the predation mortality of the first species.

```
m2_no_fishing <- getM2(sim0)[76,1,]
m2_with_fishing <- getM2(sim1)[76,1,]</pre>
```

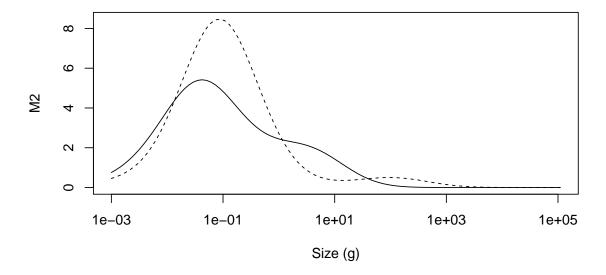


Figure 11: Predation mortalities from the unfished (dashed line) and fished (solid line) trait-based model.

The predation mortalities can then be plotted (see Figure 11).

```
plot(x = sim0@params@w, y = m2_no_fishing, log="x", type="n", xlab = "Size (g)",
     ylab = "M2")
lines(x = sim0@params@w, y = m2_no_fishing, lty=2)
lines(x = sim0@params@w, y = m2_with_fishing)
```

6.5 Setting up an industrial fishing gear

In this section we only want to operate an "industrial" fishery, like in Andersen and Pedersen (2010). Industrial fishing targets the small zooplanktivorous species that are typically used for fishmeal production.

In the previous simulations we had only one fishing gear and it targeted all the species in the community. This gear had a knife-edge selectivity that only selected species larger than 1 kg. Here we expand the model to include multiple fishing gears. This requires us to look more closely at how fishing gears are handled in mizer. In mizer it is possible for a fishing gear to catch only a subset of the species in the model. This is useful because when running a simulation with project() you can specify the effort per gear and so you can turn gears on or off as you want. The shape of the selectivity function of each gear will be the same for all of the species it catches but the selectivity parameter values for each species may be different. For example, we can set up an "industrial" gear to catch only a subset of species. Each species it catches will be caught with knife-edge selectivity but they may have a different knife-edge positions.

Using the trait-based model wrapper function it is only possible to have a knife-edge selectivity. Each

species in the model must be given the position of the knife edge and the name of the fishing gear. This is done using the knife_edge_size argument (which we have already seen) and the gear_names argument of the set_trait_model() function. In the previous examples, we passed in the knife_edge_size argument as a single value which was used for all the species. This effectively set up a single gear, that caught all species using the same selectivity pattern. The gear_names argument was not used. Now we are going to pass the knife_edge_size argument as a vector with the same length as the number of species in the model. The values in the vector will be the positions of the knife-edge for each species. We are also going to pass in a new argument, gear_names which is a vector of the names of the gears. The vector must have the same length as the number of species in the model.

We will set up the model to include two fishing gears: an "industrial" gear that only catches species with an asymptotic size less than or equal to 500g, and a second gear, "other", that catches everything else. The position of the knife-edge for both gears will occur at 0.05×10^{-5} x the asymptotic size i.e. the selectivity parameters will be different for each species and will depend on the asymptotic size.

To start with we need to know what the asymptotic sizes of the species in the model are so we can determine the knife-edge positions for each species. As mentioned above, the <code>set_trait_model()</code> function spaces the asymptotic sizes equally on a logarithmic scale. This means we can calculate them by hand.

```
no_sp <- 10
min_w_inf <- 10
max_w_inf <- 1e5
w_inf <- 10^seq(from=log10(min_w_inf), to = log10(max_w_inf), length=no_sp)</pre>
```

We can then use these asymptotic sizes to set a vector of knife-edges that are 0.05 times the asymptotic size:

```
knife_edges <- w_inf * 0.05
```

Now we want to assign each species to either the "industrial" or "other" gear, We want to create a vector of gear names. This vector must be the same length as the number of species in the model.

```
other_gears <- w_inf > 500
gear_names <- rep("Industrial", no_sp)
gear_names[other_gears] <- "Other"</pre>
```

Finally, we can create our *MizerParams* object by passing in the knife_edge_sizes and gear_names argument. All the other arguments are the same as before:

To check what has just happened we can take a look inside the *MizerParams* object. There is a slot in the object called **species_params**. This is a *data.frame* that contains the life-history parameters of the species in the model (the results of running this command are not shown):

```
params_multi_gear@species_params
```

This data.frame is pretty interesting as it allows you to investigate the parameters for each species. For example, you can see that the predator-prey mass ratio parameters, beta and sigma, are indeed

the same for each species. The columns of the species_params data.frame that we are interested in here are species (the name of the species, here just numerical identifiers), w_inf (the asymptotic size), sel_func (the name of the selectivity function for that species), knife_edge_size (the position of the knife-edge of the selectivity) and gear (the name of the fishing gear). You can see that two gears have been set up, "Industrial" and "Other" and that they catch different species depending on their asymptotic size.

Having created our *MizerParams* object with multiple gears, we can now turn our attention to running a projection with multiple gears. In our previous examples of calling project() we have specified the fishing effort with the effort argument using a single value. This fixes the fishing effort for all gears in the model, for all time steps. We can do this with our multi-gear parameter object:

```
sim_multi_gear <- project(params_multi_gear, t_max = 75, effort = 0.5)</pre>
```

By plotting this you can see that the fishing mortality for each species now has a different selectivity pattern (Figure 12), and that the position of the selectivity knife-edge is given by the asymptotic size of the species.

```
plot(sim_multi_gear)
```

For the industrial fishery we said that we only wanted species with an asymptotic size of 500 g or less to be fished. There are several ways of specifying the effort argument for project(). Above we specified a single value that was used for all gears, for all time steps. It is also possible to specify a separate effort for each gear that will be used for all time steps. To do this we pass in effort as a named vector. Here we set the effort for the "Industrial" gear to 0.75, and the effort of the "Other" gear to 0 (effectively turning it off).

```
sim_multi_gear <- project(params_multi_gear, t_max = 75,
    effort = c(Industrial = 0.75, Other = 0))</pre>
```

Now you can see that the "Industrial" gear has been operating and that fishing mortality for species larger than 500 g is 0 (Figure 13).

```
plot(sim_multi_gear)
```

6.6 The impact of industrial fishing

In the previous section we set up and ran a model in which an industrial fishery was operating that only selected smaller species. We can now answer the question: what is the impact of such a fishery? We can again compare abundances of the fished ($sim_industrial1$) and unfished ($sim_industrial0$) cases:

```
sim_industrial0 <- project(params_multi_gear, t_max = 75, effort = 0)
sim_industrial1 <- project(params_multi_gear, t_max = 75,
    effort = c(Industrial = 0.75, Other = 0))
total_abund0 <- apply(sim_industrial0@n[76,,],2,sum)
total_abund1 <- apply(sim_industrial1@n[76,,],2,sum)
relative_abundance <- total_abund1 / total_abund0</pre>
```

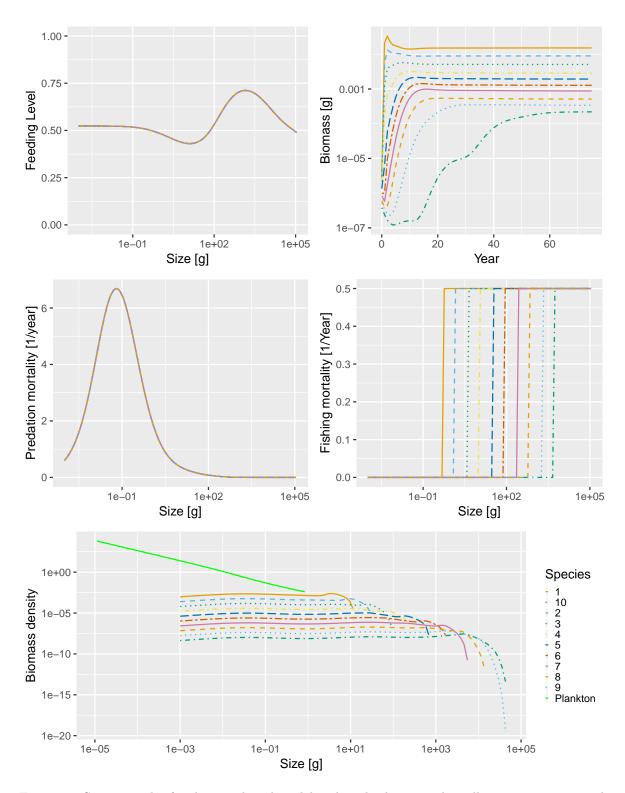


Figure 12: Summary plot for the trait-based model with multiple gears when all gears are operational.

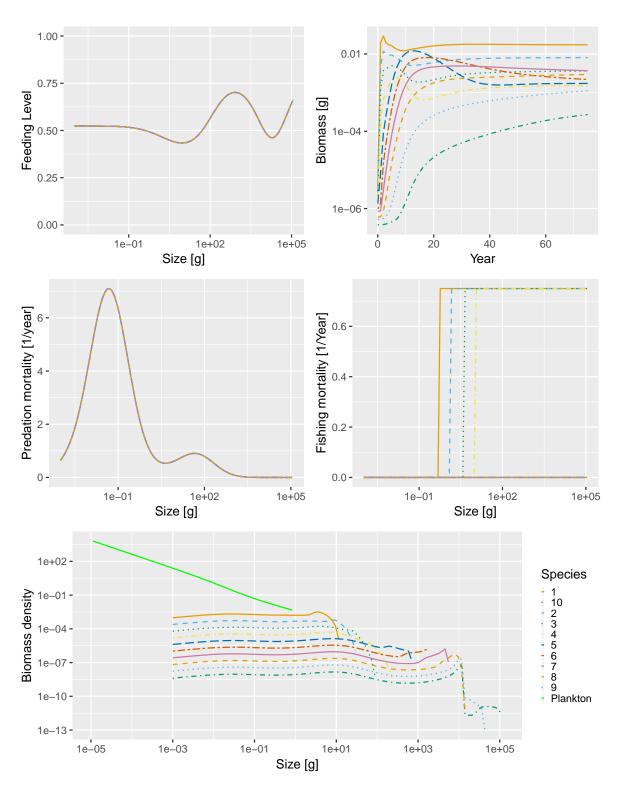


Figure 13: Summary plot for the trait-based model with multiple gears when only the industrial gear that fishes on species with asymptotic size of $500~{\rm g}$ or less is operational.

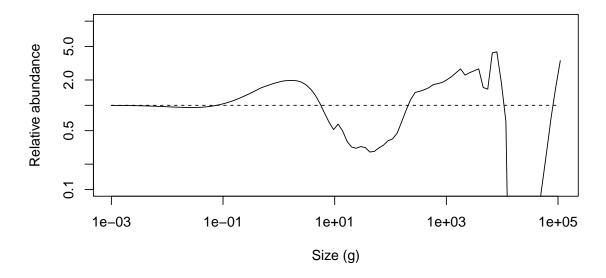


Figure 14: Relative abundances from the unfished (dashed line) and fished (solid line) trait based model with an industrial fishery that targets species with an asymptotic size of 500 g or less.

And plot the relative abundances:

```
plot(x=sim0@params@w, y=relative_abundance, log="xy", type="n", xlab = "Size (g)",
    ylab="Relative abundance", ylim = c(0.1,10))
lines(x=sim0@params@w, y=relative_abundance)
lines(x=c(min(sim0@params@w),max(sim0@params@w)), y=c(1,1),lty=2)
```

This shows another trophic cascade (Figure 14), although this time one driven by fishing the species at the midrange part of the spectrum, not the largest individuals as before. This trophic cascade acts in both directions. The cascade upwards is driven by the lack of food for predators leading to smaller realised maximum sizes. The cascade downwards has the same mechanism as fishing on large fish, a combination of predation mortality and food limitation.

7 Introducing multispecies models

The previous sections have used wrapper functions to set up *MizerParams* objects that are appropriate for community and trait-based simulations. We now turn our attention to multispecies, or species-specific, models. These are potentially more complicated than the community and trait-based models and use the full power of the mizer package.

In multispecies type models multiple species are resolved. However, unlike in the trait-based model which also resolves multiple species, explicit species are represented. There are several advantages to this approach. As well as investigating the community as a whole (as was done for the community and trait-based models), we are able to investigate the dynamics of individual species. This means

that species specific management rules can be tested and species specific metrics, such as yield, can be compared to reference levels.

A multispecies model can take more effort to set up. For example, each species will have different life-history parameters; there may be multiple gear types with different selectivities targeting different groups of species; the fishing effort of each gear may change with time instead of just being constant (which has been the case in the simulations we have looked at so far); the interactions between the species needs to be considered.

For the remainder of this vignette we build up a multispecies model for the North Sea. To effectively use mizer for a multispecies model we are going to have to take a closer look at the *MizerParams* class and the project() method. This will all be done in the context of examples so hopefully everything will be clear.

We also take a closer look at some of the summary plots and analyses that can be performed, for example, calculating a range of size-based indicators.

8 Setting up a multispecies model

8.1 Overview

The *MizerParams* class is used for storing model parameters. We have already met the *MizerParams* class when we looked at community and trait-based models. However, direct handling of the class was largely hidden by the use of the wrapper functions. To set up a multispecies model we need to directly create and use the *MizerParams* class. This is probably the most complicated part of using the mizer package so we will take it slowly. For additional help you can look at the help page for the class by entering class? MizerParams.

The MizerParams class stores the:

- life-history parameters of the species in the community, such as W_{∞} ;
- size-based biological parameters for the species, such as the search volume, V(w);
- stock-recruitment relationship functions and parameters of each species;
- interaction matrix to describe the spatial overlap of pairs of species;
- parameters relating to the growth and dynamics of the background resource spectrum;
- fishing gear parameters: selectivity and catchability.

Note that the *MizerParams* class does not store any parameters that can vary through time, such as fishing effort or population abundance. These are stored in the *MizerSim* class which we will come to later in Section 9.

Although the *MizerParams* class seems complicated, it is relatively straightforward to set up and use. Objects of class *MizerParams* are created using the constructor method MizerParams(). This constructor method can take many arguments. However, creation is simplified because many of the arguments have default values.

In the rest of this section we look at the main arguments to the MizerParams() constructor method. To help understand how the constructor is used and how the *MizerParams* class relates to the equations given in Section 3, there is an example section where we create example parameter objects using data that comes with the mizer package.

8.2 The species parameters

Although many of the arguments used when creating a $\it MizerParams$ object are optional, there is one argument that must be supplied by the user: the $\it species$ $\it specific parameters$. These are stored in a single $\it data.frame$ object. The $\it data.frame$ is arranged species by parameter, so each column is a parameter and each row has the parameters for one of the species in the model. Although it is possible to create the data.frame by hand in R, it is probably easier to create the data externally as a .csv file (perhaps using a suitable open source spreadsheet such as LibreOffice) and then read the data into R.

For each species in the model community there are certain parameters that are essential and that do not have default values. The user must provide values for these parameters. There are also some essential parameters that have default values, such as the selectivity function parameters, and some that are calculated internally using default relationships if not explicitly provided. These defaults are used if the parameters are not found in the data frame. A description of the columns of the species parameter data frame and any default values can be seen Table 2.

The essential columns of the species parameters data frame that have no default values are: species, the names of the species in the community; w_inf, the asymptotic mass of the species; w_mat, the mass at maturation; beta and sigma, the predator-prey mass ratio parameters β and σ (see Equation 3.3); stock-recruitment parameters (by default, the stock-recruitment function is a Beverton-Holt type and so, unless a different SRR function is used, a r_max column must be provided - see Section 8.4 for more details).

Essential columns that have default values are: k, the activity coefficient (default = 0); alpha, the assimilation efficiency (default = 0.6); erepro, the reproductive efficiency (default value = 1); w_min, the size of recruits (default value is the smallest size of the community size spectrum); sel_func, the name of the fishing selectivity function (default value = "knife_edge"); gear, the name of the fishing gear that catches the species (default value is the name of the species in the species column); catchability, the catchability of the fishing gear on that species (default value = 1). Additionally, columns that contain the selectivity function parameters are needed. As mentioned, the default selectivity function is a "knife_edge" function. This has an argument knife_edge_size that determines the knife-edge position and has a default value of w_min. If any of these columns are not included in the species parameter data.frame, the default values are used.

As mentioned above, there are some columns that are essential but if they are not provided, values for them are estimated using the values in the other columns. These columns are: h, the maximum food intake; gamma, the volumetric search rate; ks, the coefficient for standard metabolism; z0, the mortality from other sources ($\mu_{b,i}$ in Equation 3.14). These parameters can be included as columns in the species parameters data.frame if they are available. If they are not provided then the MizerParams() construction method will try to calculate them.

The h column is calculated as:

$$h = \frac{3k_{vb}}{\alpha f_0} W_{\infty}^{1/3} \tag{8.1}$$

where k_{vb} is the von Bertalanffy K parameter and f_0 is the feeding level of small individuals feeding mainly on the background resource. This mean that if an h column is not included in the species parameter data.frame, a column for k_vb is necessary. If it is not included then the MizerParams() method will fail with an error message. The calculation also requires a value of the feeding level of small individuals. This can be passed as an additional argument, f0, to the MizerParams() constructor and it has a default value of 0.6.

The gamma column is calculated using Equation 3.17. This calculation requires that the h column is available, either included in the species parameter data.frame, or calculated internally using the k_vb

column as described above. This means that if you include a k_vb column in the data.frame, h and gamma will be calculated from it.

The z0 column (mortality from other sources) is calculated using Equation 3.14. z0pre (equivalent to μ_0) and z0exp (the power that W_{∞} is raised to) can be passed as arguments to the MizerParams() constructor and have default values of 0.6 and n-1 (n has a default value of 2/3 - see below) respectively.

The ks column is calculated as 20% of h, i.e. the standard metabolism coefficient is 20% of the maximum consumption. Standard metabolism is used in calculation of the growth of individuals as $ks * w_i^p$ (see Section 3.4).

You can see in Table 2 that most of the species specific parameters relate to the life history of the species. The others relate to the gear selectivity function and the stock-recruitment relationship. These are explained further in Sections 8.3 and 8.4 respectively.

8.3 Fishing gears and selectivity

In this section we take a look at how fishing is implemented and how fishing gears are set up within mizer.

In mizer, fishing mortality is imposed on species by fishing gears. The total fishing mortality is obtained by summing over the mortality from all gears,

$$\mu_{f,i}(w) = \sum_{g} F_{g,i}(w),$$
(8.2)

where the fishing mortality $F_{g,i}(w)$ imposed by gear g on species i at size w is calculated as:

$$F_{q,i}(w) = S_{q,i}(w)Q_{q,i}E_q$$
 (8.3)

where S is the selectivity by species, gear and size, Q is the catchability by species and gear and E is the fishing effort by gear. The selectivity at size has a range between 0 (not selected at that size) to 1 (fully selected at that size). Catchability is used as an additional scalar to make the link between gear selectivity, fishing effort and fishing mortality. For example, it can be set so that an effort of 1 gives a desired fishing mortality. In this way effort can then be specified relative to a 'base effort', e.g. the effort in a particular year. Fishing effort is not stored in the MizerParams object. Instead, effort is set when the simulation is run and can vary through time (see Section 9).

At the moment a species can only be selected by one fishing gear, although each gear can select more than one species (this is a limitation with the current package that will be developed in future releases).

The selectivity at size of each gear is given by a selectivity function. Some selectivity functions are included in the package. New functions can be defined by the user. Each gear has the same selectivity function for all the species it selects, but the parameter values for each species may be different, e.g. the lengths of species that a gear selects may be different.

The name of the selectivity function is given by the sel_func column in the species parameters data.frame. Each selectivity function has a range of arguments. Values for these arguments must be included as columns in the species parameters data.frame. The names of the columns must exactly match the names of the arguments. For example, the default selectivity function is <code>knife_edge</code> which has sudden change of selectivity from 0 to 1 at a certain size. The arguments for this selectivity function can be seen in the help page for this function. To see them enter:

?knife_edge

It can be seen that the knife_edge() function has arguments w and knife_edge_size The first argument, w, is size (the function calculates selectivity at size). All selectivity functions must have w as the first argument. The values for the other arguments must be found in the species parameters data.frame. So for the knife_edge() function there should be a knife_edge_size column (but note that because knife_edge() is the default selectivity function, the knife_edge_size argument actually has a default value = w_mat). This can be seen in the example in Section 8.7. If the columns of the selectivity function arguments are not in the species parameter data.frame, an error is thrown when the MizerParams object is created.

Users are able to write their own size based selectivity function. The first argument to the function must be w and the function must return a vector of the selectivity (between 0 and 1) at size.

The name of the fishing gear is given in the gear column of the species parameter data.frame. If the gear column is not specified, the default gear name is simply the name of the species. This implies that each species is fished by a different gear. This approach can be used to explore the impacts of changing fishing mortality on individual species.

8.4 The stock-recruitment relationship

In size spectrum modelling recruitment refers to the flux of individuals that enter the size-spectrum at the smallest size group of that species (given by the parameter w_min in the species parameter data.frame). As can be seen in Section 3, calculating the recruitment flux involves calculating the "density independent" recruitment, $R_{p.i}$ (see Section 3.5). The $R_{p.i}$ is then modified by a stock-recruitment relationship (SRR) to impose some form of density-dependence. This then results in the density-dependent recruitment, R_i (see Section 3.6). Without this density dependence, the realised recruitment flux to the smallest size class is determined only by $R_{p.i}$. The default SRR is a Beverton-Holt type function (see Equation 3.12).

Similar to the fishing selectivity functions, any parameter used in the stock-recruitment function, other than $R_{p.i}$, must be in the species parameter data frame and the column must have the same name as the function argument. For example, the default stock-recruitment function has a second argument to it, r_max. Therefore the species parameter data frame must have an r_max column.

Users are able to write their own stock-recruitment function. The first argument to the function must be rdi, which is the density independent recruitment $R_{p,i}$, the second argument must be $species_params$, the dataframe with the species parameters. This function should then be assigned to the srr slot of the MizerParams object.

8.5 The interaction matrix

The interaction matrix describes the interaction of each pair of species in the model. This can be viewed as a proxy for spatial interaction e.g. to model predator-prey interaction that is not size based. The values in the interaction matrix are used to scale the encountered food and predation mortality (see Section 3.2). The matrix is square with every element being the interaction between a pair of species. The dimensions, nrows and ncolumns, therefore equal the number of species. The values are between 0 (species do not overlap and therefore do not interact with each other) to 1 (species overlap perfectly). If all the values in the interaction matrix are set to 1 then predator-prey interactions are determined entirely by size-preference.

The interaction matrix must be of type *array* or *matrix*. One way of creating your own is to enter the data using a spreadsheet (such as LibreOffice) and saving it as a .csv file. The data can be read into R using the command read.csv(). This reads in the data as a data.frame. We then need to convert this to a matrix using the as() function. An example of how to do this is given in Section 8.7.

It should be noted that the order of species in the interaction matrix has to be the same as the order in the species parameters data.frame. Although you can specify the dimnames of the interaction matrix, these names are overwritten by the species names from the species parameters data.frame inside the *MizerParams* constructor.

If an interaction matrix is not specified to the MizerParams() constructor the default iteration matrix is used. This has all values set to 1.

8.6 The other MizerParams() arguments

As well as the essential species parameters data frame and the interaction matrix, there are several other arguments to the MizerParams constructor. These have default values. The arguments can be seen in Table 3.

Some of these parameters may be used to calculate the species specific parameters if they are not provided. For example, if there is no gamma column in the species parameter data.frame, then it is calculated using kappa and f0. This means that depending on which columns have been provided in the species parameters data.frame, some of the parameters in Table 3 may not be used. For example, if the column z0 (the mortality from other sources) has been included, then the arguments z0pre and z0exp are not used.

Determining a value for the kappa argument can be difficult and may need to be estimated through some kind calibration process. The default value kappa is for the North Sea model.

8.7 Examples of making a *MizerParams* objects

As mentioned in the preceding sections, an object of *MizerParams* is created by using the MizerParams() constructor method. You can see the help page for the constructor:

```
help(MizerParams)
```

This shows that the constructor takes the following arguments:

object The species parameter data.frame (see Section 8.2). This is compulsory with no default value.

inter The interaction matrix (see Section 8.5). The default is a matrix of 1s.

... Other model parameters (see Section 8.6).

In the rest of this section we demonstrate how to pull these elements together to make *MizerParams* objects.

The first step is to prepare the species specific parameter data.frame. As mentioned above, one way of doing this is to use a spreadsheet and save it as a .csv file. We will use this approach here. An example .csv file has been included in the package. This contains the species parameters for a multispecies North Sea model (Blanchard et al., 2014). This file is placed in the doc folder of the package installation. The location of the file can be found by running:

```
system.file("doc/NS_species_params.csv",package="mizer")
```

This file can be opened with most spreadsheets or a text editor for you to inspect. This can be loaded into R using the following code (after you have told R to look in the right directory):

```
params_data <- read.csv("NS_species_params.csv")</pre>
```

This reads the .csv file into R in the form of a data.frame. You can check this with the class:

```
class(params_data)
## [1] "data.frame"
```

The example data.frame can be inspected by entering the name of the object.

```
params_data
##
                                           r_max k_vb
      species w_inf w_mat
                            beta sigma
                                    0.8 7.38e+11 0.681
## 1
        Sprat
                 33
                       13 51076
## 2
      Sandeel
                 36
                        4 398849
                                    1.9 4.10e+11 1.000
## 3
                100
                       23
       N.pout
                              22
                                   1.5 1.05e+13 0.849
## 4
      Herring
                334
                       99 280540
                                    3.2 1.11e+12 0.606
## 5
          Dab
                324
                       21
                              191
                                    1.9 1.12e+10 0.536
## 6
               1192
                       75
                              22
                                    1.5 5.48e+11 0.323
      Whiting
## 7
         Sole
                866
                       78
                              381
                                    1.9 3.87e+10 0.284
                              283
## 8
     Gurnard
                668
                       39
                                    1.8 1.65e+12 0.266
       Plaice
               2976
                      105
                              113
                                    1.6 4.08e+14 0.122
## 10 Haddock 3485
                      165
                              558
                                    2.1 1.84e+12 0.271
## 11
          Cod 40044
                     1606
                               66
                                    1.3 8.26e+09 0.216
## 12 Saithe 16856
                     1076
                              40
                                    1.1 1.12e+11 0.175
```

You can see that there are 12 species and 7 columns of parameters: species, w_inf,w_mat,beta,sigma,r_max and k_vb.

Of these parameters, species, w_inf, w_mat, beta and sigma are essential and have no default values (as described in Section 8.2). r_max is a SRR parameter. We are going to use the default Beverton-Holt type SRR which has r_max as an argument (see Section 8.4), making this column also essential. The final column, k_vb, will be used to calculate values for h and then gamma. This column is only essential here because the h and gamma are not included in the data.frame. It would also have been possible to include h and gamma columns in the data.frame and not include the k_vb column.

The values of the non-essential species specific parameters alpha, k, ks, z0, w_min and erepro are not included in the data.frame. This means that the default values will be automatically used when we create the *MizerParams* object.

Note that there are no columns describing the fishing selectivity. There is no sel_func column to determine the selectivity function. This means that the default selectivity function, knife_edge, will be used. As mentioned in Section 8.3, this function also needs another argument, knife_edge_size. This is not present in the data.frame and so it will be set to the default value of w_mat. Also, there is no catchability column so a default value for catchability of 1 will be used for all gears and species.

This species parameter data frame is the minimum we need to create a *MizerParams* object as it contains only essential columns. To create the *MizerParams* object we pass the data frame into the MizerParams() constructor method:

```
params <- MizerParams(params_data)
```

We have just created a *MizerParams* object:

```
class(params)

## [1] "MizerParams"

## attr(,"package")

## [1] "mizer"
```

As has been mentioned in Sections 5 and 6, a *MizerParams* object is made up of "slots" that store a wide range of model parameters. Each of these slots contains information on the parameters in the model. A description of these slots can be found by calling help() on the class: help("MizerParams-class"). The different slots can be accessed using the @ operator.

The slot species_params contains the species parameters data.frame that was passed in to the constructor. We can inspect this slot with:

```
params@species_params
                                                          gear k alpha
          species w_inf w_mat
                              beta sigma
                                            r_max k_vb
## Sprat
            Sprat 33 13 51076 0.8 7.38e+11 0.681
                                                         Sprat 0
                                                                  0.6
## Sandeel Sandeel 36 4 398849 1.9 4.10e+11 1.000 Sandeel 0
                                                                  0.6
         N.pout 100 23
                                22 1.5 1.05e+13 0.849 N.pout 0
## N.pout
                                                                  0.6
## Herring Herring 334 99 280540
                                    3.2 1.11e+12 0.606 Herring 0
                                                                  0.6
## Dab
         Dab 324 21 191 1.9 1.12e+10 0.536
                                                           Dab 0
                                                                  0.6
                               22 1.5 5.48e+11 0.323 Whiting 0
## Whiting Whiting 1192 75
                                                                  0.6
                        78 381 1.9 3.87e+10 0.284
## Sole
        Sole
                  866
                                                          Sole 0
                                                                  0.6
## Gurnard Gurnard 668
                        39 283 1.8 1.65e+12 0.266 Gurnard 0
                                                                  0.6
## Plaice Plaice 2976 105 113 1.6 4.08e+14 0.122 Plaice 0
                                                                  0.6
## Haddock Haddock 3485 165 558 2.1 1.84e+12 0.271 Haddock 0
                                                                  0.6
                              66 1.3 8.26e+09 0.216 Cod 0
## Cod Cod 40044 1606
                                                                  0.6
## Saithe Saithe 16856 1076
                                40 1.1 1.12e+11 0.175 Saithe 0
                                                                  0.6
##
   erepro sel_func knife_edge_size
                                           h
                                                       gamma
                                                                      z0
            1 knife_edge
                                      13 18.20276 3.190183e-11 0.18705957
## Sprat
4 27.51606 1.503569e-11 0.18171206
                                      23 32.83924 8.504085e-11 0.12926608
                                     99 35.03807 1.123212e-11 0.08647736
          1 knife_edge
1 knife_edge
1 knife_edge
                                     21 30.67834 4.645215e-11 0.08735805
## Dab
## Whiting
                                       75 28.53952 7.390625e-11 0.05658819
## Sole
                                      78 22.55847 3.115287e-11 0.06294752
## Gurnard 1 knife_edge
## Plaice 1 knife_edge
## Haddock 1 knife_edge
## Cod 1 knife_edge
                                     39 19.37727 2.948552e-11 0.06863713
                                    105 14.62366 2.846500e-11 0.04171321
                                      165 34.23910 4.037031e-11 0.03957464
                                    1606 61.58170 1.597275e-10 0.01753768
## Saithe
             1 knife_edge
                                     1076 37.39168 1.230565e-10 0.02340093
##
                ks w_min w_min_idx
## Sprat
           3.640551 0.001
                                1
## Sandeel 5.503212 0.001
                                1
## N.pout 6.567848 0.001
```

```
## Herring 7.007614 0.001
                                    1
## Dab
            6.135668 0.001
## Whiting
            5.707904 0.001
                                    1
## Sole
            4.511695 0.001
                                    1
## Gurnard
            3.875454 0.001
                                    1
## Plaice
            2.924733 0.001
                                    1
## Haddock 6.847819 0.001
                                    1
## Cod
           12.316339 0.001
                                    1
## Saithe 7.478336 0.001
```

We can see that this contains the original species data.frame (with $w_{\tt inf}$ and so on), plus any default values that may not have been included in the original data.frame. For example, we can see that there are no columns for alpha and h and gamma etc.

Also note how the default fishing gears have been set up. Because we did not specify gear names in the original species parameter data.frame, each species is fished by a unique gear named after the species. This can be seen in the new gear column which holds the names of the fishing gears. Also, the selectivity function for each fishing gear has been set in the sel_func column to the default function, knife_edge(). A catchability column has been added with a default value of 1 for each of the species that the gear catches. An example of setting the catchability by hand can be seen in Section 11.

As has been shown in Sections 5 and 6, there is a summary() method for *MizerParams* objects which prints a useful summary of the model parameters:

```
summary(params)
```

As well as giving a summary of the species in the model and what gear is fishing what species, it gives a summary of the size structure of the community. For example there are 100 size classes in the community, ranging from 0.001 to 4.4×10^4 . These values are controlled by the arguments no_w , min_w and max_w respectively. For example, if we wanted 200 size classes in the model we would use:

```
params200 <- MizerParams(params_data, no_w=200)
summary(params200)</pre>
```

So far we have created a *MizerParams* object by passing in only the species parameter data.frame argument. This means the interaction matrix will be set to the default value (see Section 8.5). This is a matrix of 1s, implying that all species fully interact with each other, i.e. the species are spread homogeneously across the model area. For the North Sea this is not the case and so the model would be improved by also including an interaction matrix which describes the spatial overlap between species (see Section 8.5).

An example interaction matrix for the North Sea has been included in mizer as a .csv file. The location of the file can be found by running:

```
system.file("doc/inter.csv",package="mizer")
```

Take a look at it in a spreadsheet if you want. As mentioned above, to read this file into R we can make use of the read.csv() function. However, this time we want the first column of the .csv file to be the row names. We therefore use an additional argument to the read.csv() function: row.names.

```
inter <- read.csv("inter.csv", row.names=1)</pre>
```

The read.csv() function reads the data into a data frame. We want the interaction matrix to be of class *matrix* so we need to make use of the as() function.

```
inter <- as(inter, "matrix")</pre>
```

We now have an interaction matrix that can be passed to the *MizerParams* constructor along with the species parameter data.frame. To make the *MizerClass* object you just call the constructor method and pass in the arguments. We will use default values for the remainder of the arguments to the MizerParams() method (see Section 8.6 and Table 3). This means that we only need to pass in two arguments to the constructor:

```
params <- MizerParams(params_data, interaction = inter)</pre>
```

Note that the first argument must be the species parameters data frame. The remaining arguments can be in any order but should be named. If we didn't want to use default values for the other arguments we would pass them in to the constructor by name.

We now have all we need to start running projections. Before we get to that though, we'll take a quick look at how different fishing gears can be set up.

8.8 Setting different gears

In the above example, each species is caught by a different gear (named after the species it catches). This is the default when there is no **gear** column in the species parameter data.frame.

Here, we look at an example where we do specify the fishing gears. We take the original params_data species parameter data.frame that was read in above and bind an additional column, gear, to it. This gear column contains the name of the gear that catches the species in that row. Here we set up four different gears: Industrial, Pelagic, Beam and Otter trawl, that catch different combinations of species.

If you inspect the params_data object you will see a new column, gear, has been added to it. We then make a new *MizerParams* object as before:

```
params_gears <- MizerParams(params_data_gears, interaction = inter)</pre>
```

You can see the result by calling summary() on the params_gears object.

In this example the same gear now catches multiple stocks. For example, the "Industrial" gear catches Sprat, Sandeel and Norway Pout. Why would we want to set up the gears like this? In the next section we will see that to project the model through time you can specify the fishing effort for each gear through time. By setting the gears up in this way you can run different management scenarios of changing the efforts of the fishing gears rather than on individual species. It also means that after a simulation has been run you can examine the catches by gear.

9 Running a simulation

In the preceding section and in the sections on the community and trait-based models above, we used the project() method to perform simple simulations where the fishing effort was held constant throughout the duration of the simulation. In the trait-based model example, we also looked at how the effort for different gears could be specified. In this section we take a detailed look at how the project() method works and the different ways in which effort and time can be set up.

In mizer, simulations are performed using the project() method. This method takes a *MizerParams* object and projects it forward through time, starting from an initial population abundance and with a pre-determined fishing effort pattern.

Running a projection with project() requires various arguments:

A *MizerParams* object The model parameters (see previous section);

Fishing effort The fishing effort of each gear through time;

Initial population The initial abundances of the stocks and the background spectrum;

Time arguments Arguments to control the time of the simulation, including the simulation time step, the length of the simulation and how frequently the output is stored.

The help page for project() describes the arguments in more detail.

The *MizerParams* class was explored in the previous section. In this section we will look at the other arguments and use examples to perform some simple projections.

The object returned from calling project() is of class *MizerSim*. This contains the abundances of the species in the model by time and size. It is described fully in Section 9.4.

9.1 The time arguments

There are three arguments that control time in the project() method: dt, t_max and t_save. All of them have default values.

t_max determines the maximum time of the simulation, i.e. how long the projection is run for. The default value for t_max is 100 respectively.

dt is the time step used by the numerical solver in project(). This is the time step on which the model operates. The smaller the value, the longer the model will take to run. However, sometimes it is necessary to use a small value to avoid numerical instabilities. The default value is 0.1.

The final argument is t_save. This sets how frequently project() stores the state of the model in the resulting *MizerSim* object. For example, if t_save = 2, the state of the model is stored at t = 0, 2, 4... etc. t_save must be a multiple of dt. The default value of t_save is 1.

9.2 Setting the fishing effort

The fishing effort argument describes the effort of the fishing gears in the model through time. We have already seen that information on the fishing gears and their selectivities and catchabilities is stored in the MizerParams argument.

There are three ways of setting the fishing effort. Examples of all three can be seen in Section 9.5.

The simplest way is by passing the effort argument as a single number. This value is then used as the fishing effort by all of the gears at each time step of the projection, i.e. fishing effort is

constant throughout the simulation and is the same for all gears. We have seen this method in the community and trait-based model sections above. The length of the simulation is determined by the t_max argument (see Section 9.1).

The second method for setting the fishing effort is to use a numeric vector that has the same length as the number of gears. The values in the vector are used as the fishing effort of each gear at each time step, i.e. again, the fishing effort is constant through time but now each gear can have a different constant effort. The effort vector must be named and the names must be the same as the gears in the MizerParams object. Again, the length of the simulation is determined by the t_max argument.

Finally, the most sophisticated way of setting the fishing effort is to use a two-dimensional array or matrix of values, set up as time step by gear. Each row of the array has the effort values of each fishing gear by time. The array must have dimension names. The names of the first dimension (the row names) are the times. The steps between the times can be greater than the dt argument but must be contiguous. The names of the second dimension (the column names) must match the names of the gears in the *MizerParams* object used in the projection.

It is not necessary to supply a t_max argument when the effort is specified as an array because the maximum time of the simulation is taken from the dimension names. If a value for t_max is also supplied it is ignored.

9.3 Setting the initial population abundance

When running a simulation with the project() method, the initial populations of the species and the background spectrum need to be specified. These are passed to project() as the arguments initial_n and initial_n_pp respectively. initial_n is a matrix (with dimensions species x size) that contains the initial abundances of each species at size (the sizes must match those in the species size spectrum). initial_n_pp is a vector of the same length as the the length of the full spectrum (which can be seen as slot w_full in the MizerParams object).

By default, the initial_n argument has values automatically calculated by the function get_initial_n(). The default value for initial_n_pp is the carrying capacity of the background spectrum, stored in the cc_pp slot of the *MizerParams* parameters object.

9.4 What do you get from running project()?

Running project() returns an object of type *MizerSim* that stores the results of the projection. Like the *MizerParams* class this is also made up of various "slots", which can be accessed using the @ operator. An object of *MizerSim* has four slots, details of which can be seen in the help page (help("MizerSim-class"). The params slot holds the *MizerParams* object that was passed in to project(). The effort slot holds the fishing effort of each gear through time. Note that the effort slot may not be exactly the same as the effort argument that was passed in to project(). This is because only the saved effort is stored (the frequency of saving is determined by the argument t_save). The n and n_pp slots hold the saved abundances of the species and the background population at size respectively.

9.5 Projection examples

In this section we'll look at how to run simulations with the project() method. The examples will focus on how fishing effort can be specified in different ways. The results of the simulations will not be explored in detail. We will leave that for Section 10.2.

Remember that the fishing mortality by size on a species is the product of the selectivity, the catchability and the effort of the gear that caught it (see Equation 8.3). We have not specified any catchability values in the species parameter data frame so the default value of 1 is used. The selectivity ranges between 0 and 1. This means that in these examples the fishing mortality of a fully selected species is given by the effort of the gear that catches it.

9.5.1 Projections with single, simple constant effort

When we use a single value for the effort argument, the value is used as a constant effort for all the gears. This method can be particularly useful for quickly projecting forward without fishing (you just set the effort argument to 0).

We will use the params object that was created in Section 8.7 in which each species is caught by a separate gear. Here we make the object again:

```
params <- MizerParams(params_data, interaction = inter)</pre>
```

As described above, effort is associated with fishing gears. Because we haven't specified any gears in the params_data species parameter data.frame, each species is caught by a separate gear, named after the species.

As well as thinking about the effort argument we also need to consider the time parameters. We will project the populations forward until time equals $10 \text{ (t_max} = 10)$, with a time step of 0.1 (dt = 0.1), saving the output every time step (t_save = 1). We use a constant effort value of 1.0.

```
sim <- project(params, effort = 1, t_max = 10, dt = 0.1, t_save = 1)</pre>
```

The resulting sim object is of class *MizerSim*. At this point we won't explore how the results can be investigated in detail. However, we will use the basic summary plot that you have seen before:

```
plot(sim)
```

Without fishing the community settles down to equilibria at about t=50 (Figure 15). The big difference between this multispecies model and the trait-based model can be seen in the range of M2 and feeding level values. With the trait-based model all the "species" had the same M2 and feeding level patterns (see Figure 8). Here the species all have different patterns, driven by their differing life history characteristics and the heterogeneous interaction matrix.

You can also see in Figure 15 that each species has different fishing selectivity (see the Total fishing mortality panel). Remember that the default setting for the fishing gears is a knife-edge gear where the knife-edge is positioned at the species w_mat parameter.

The effort through time can be inspected by looking at the effort slot (we use the head() function to just show the first few lines). The effort slot shows the effort by time and gear. You can see here that each species is caught by a separate gear, and the gear is named after the species. In this example, we specified the effort argument as a single numeric of value 1. As you can see this results in the same effort being used for all gears for all time steps:

```
head(sim@effort)

## gear

## time Sprat Sandeel N.pout Herring Dab Whiting Sole Gurnard Plaice Haddock
```

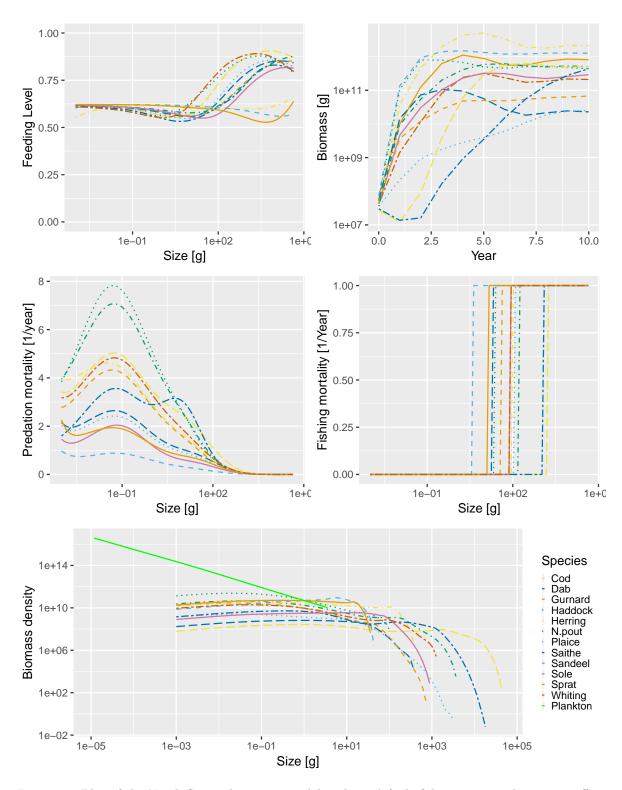


Figure 15: Plot of the North Sea multispecies model with no default fishing gears and constant effort of 1.

```
##
##
                1
                           1
                                    1
                                               1
                                                     1
                                                               1
                                                                      1
                                                                                 1
                                                                                           1
        1
                                                                                                     1
##
        2
                1
                           1
                                    1
                                               1
                                                     1
                                                               1
                                                                      1
                                                                                 1
                                                                                          1
                                                                                                     1
##
        3
                1
                           1
                                    1
                                               1
                                                     1
                                                               1
                                                                      1
                                                                                 1
                                                                                           1
                                                                                                     1
                                               1
                                                     1
                                                               1
                                                                      1
                                                                                 1
##
                1
                           1
                                    1
                                                                                          1
                                                                                                     1
##
        5
                1
                           1
                                    1
                                               1
                                                     1
                                                               1
                                                                      1
                                                                                 1
                                                                                           1
                                                                                                     1
##
         gear
##
    time Cod Saithe
##
             1
                      1
        0
##
             1
                       1
##
        2
             1
                      1
##
        3
             1
                       1
##
        4
             1
                       1
```

A summary() method is also available for objects of type *MizerSim*. This is essentially the same as the summary for *MizerParams* objects, but includes information on the simulation time parameters.

```
summary(sim)
```

If we decrease t_save but keep t_max the same then we can see that the time dimension of the effort slot changes accordingly. This will also be true of the n and n_pp slots. Here we reduce t_save to 0.5, meaning that the effort and abundance information is stored at t = 1.0, 1.5, 2.0 etc.

```
sim <- project(params_gears, effort = 1, t_max = 10, dt = 0.1, t_save = 0.5)</pre>
head(sim@effort)
##
         gear
##
   time Industrial Pelagic Beam Otter
##
                    1
                             1
                                  1
##
     0.5
                    1
                             1
                                  1
                                         1
##
     1
                    1
                             1
                                  1
                                         1
##
     1.5
                    1
                             1
                                  1
                                         1
##
     2
                    1
                             1
                                  1
                                         1
##
```

9.5.2 Setting constant effort for different gears

As mentioned above, we can also set the effort values for each gear separately using a vector of effort values. This still keeps the efforts constant through time but it means that each gear can have a different constant effort.

Here we will use the MizerParams object with four gears, params_gears, that we created in Section 8.8. The names of the gears are Industrial, Pelagic, Beam, Otter. We need to create a named vector of effort, where the names match the gears. For example, here we want to switch off the industrial gear (i.e. effort = 0), keep the pelagic gear effort at 1, set the effort of the beam trawl gears to 0.3 and the effort of the otter trawl gear to 0.7. We set the effort like this:

```
effort <- c(Industrial = 0, Pelagic = 1, Beam = 0.3, Otter = 0.7)
```

We then call project() with this effort and inspect the resulting effort slot (again we use the head() function to just show the first few lines):

```
sim <- project(params_gears, effort = effort, t_max = 10, dt = 1, t_save = 1)</pre>
head(sim@effort)
##
##
   time Industrial Pelagic Beam Otter
                               0.3
##
                   0
                            1
                                      0.7
##
                   0
                            1
                               0.3
                                      0.7
      1
       2
                   0
##
                            1
                               0.3
                                      0.7
##
       3
                   0
                            1
                               0.3
                                      0.7
##
       4
                   0
                            1
                               0.3
                                      0.7
##
       5
                   \cap
                            1
                               0.3
                                      0.7
```

You can see that the effort for each gear is constant but each gear has the effort that was specified in the effort argument.

This impact of this can be seen plotting the fishing mortality. There is a dedicated plot, plotFMort(), that shows the fishing mortality at size for each species at a particular time step (the default is the final time step). The fishing mortality on each of the species is determined by the effort of the gear that caught it (Figure 16).

```
plotFMort(sim)
```

9.5.3 An example of changing effort through time

In this example we set up a more complicated fishing effort structure that allows the fishing effort of each gear to change through time. As mentioned above, to do this, effort must be supplied as a two dimensional array or matrix. The first dimension is time and the second dimension is gear. The dimensions must be named. The gear names must match the gears in the *MizerParams* object. Also, as mentioned above, if effort is passed in as an array then the length of the simulation is determined by the time dimension names and the argument t_max is not used. Instead the simulation runs from the earliest time in the effort array to the latest.

Here, we will use the params_gears object we created in Section 8.8 which has four gears. The names of the gears are Industrial, Pelagic, Beam, Otter.

In this example, we will project forward from time t = 1 to time t = 10. The effort of the industrial gear is held constant at 0.5, the effort of the pelagic gear is increased linearly from 1 to 2, the effort of the beam trawl decreases linearly from 1 to 0, whilst the effort of the otter trawl decreases linearly from 1 to 0.5.

First we create the empty effort array:

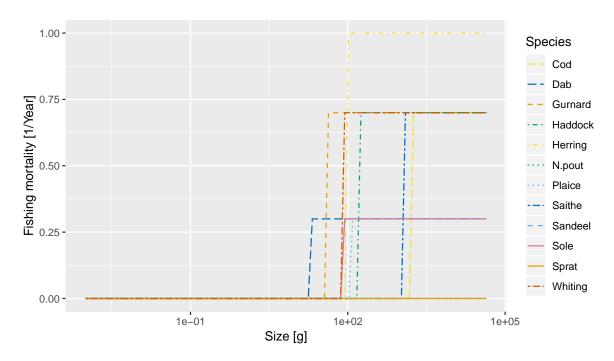


Figure 16: An example of using the plotFMort() method to show how different efforts for different gears can be specified.

Then we fill it up, one gear at a time, making heavy use of the seq() function to create a sequence:

```
effort_array[,"Industrial"] <- 0.5
effort_array[,"Pelagic"] <- seq(from = 1, to = 2, length = length(times))
effort_array[,"Beam"] <- seq(from = 1, to = 0, length = length(times))
effort_array[,"Otter"] <- seq(from = 1, to = 0.5, length = length(times))</pre>
```

The first few rows of the effort array are shown as an illustration:

```
head(effort_array)
##
       gear
##
   time Industrial Pelagic
                                  Beam
                                           Otter
               0.5 1.000000 1.0000000 1.0000000
##
##
      2
               0.5 1.111111 0.8888889 0.9444444
##
      3
               0.5 1.222222 0.7777778 0.8888889
##
               0.5 1.333333 0.6666667 0.8333333
##
      5
               0.5 1.444444 0.5555556 0.7777778
               0.5 1.555556 0.4444444 0.7222222
```

The first row gives the effort between times 1 and 2, the second between times 2 and 3, and so on. The time 10 row in the array is not actually used, except to set the final time for the simulation. Now we can use this effort array in the projection:

```
sim <- project(params_gears,effort=effort_array, dt=0.1, t_save = 1)
head(sim@effort)
##
##
   time Industrial Pelagic
                                  Beam
                                            Otter
##
               0.5 1.000000 1.0000000 1.0000000
##
      2
               0.5 1.111111 0.8888889 0.9444444
##
      3
               0.5 1.222222 0.7777778 0.8888889
               0.5 1.333333 0.6666667 0.8333333
##
      4
##
               0.5 1.444444 0.5555556 0.7777778
               0.5 1.555556 0.4444444 0.7222222
##
      6
```

As you can see, it can be quite fiddly to set up a complicated effort array so it may be easier to prepare it in advance as a .csv file and read it in, similar to how we read in the interaction matrix in Section 8.7. We give an example of this in Section 11.

Note that in this example we set up the effort array so that the effort was set every whole time step (e.g. time = 1, 2, etc). This does not have to be the case and it is possible to set the effort more frequently than that, e.g. at time = 1.0, 1.5, 2.0, 2.5 etc. The only restriction is that the difference between time dimension names must be at least as big as the dt argument.

10 Exploring the simulation results

In the previous sections we saw how to set up a model and project it forward through time under our desired fishing scenario. The result of running a projection is an object of class *MizerSim*. What do we then do? How can we explore the results of the simulation? In this section we introduce a range of summaries, plots and indicators that can be easily produced using methods included in mizer.

We will use the same ${\it MizerSim}$ object for these examples:

```
sim <- project(params_gears,effort=effort_array, dt=0.1, t_save = 1)</pre>
```

10.1 Directly accessing the slots of MizerSim objects

We have seen in previous sections that a *MizerSim* object is made up of various "slots" that contain the original parameters (species_params), the population abundances (n), the abundance of the background resource spectrum (n_pp) and the fishing effort (effort).

The projected species abundances at size through time can be seen in the n slot. This is a three-dimensional array (time x species x size). Consequently, this array can get very big so inspecting it can be difficult. In the example we have just run the time dimension of the n slot has 10 rows (one for the initial population and then one for each of the saved time steps). There are also 12 species each with 100 sizes. We can check this by running the dim() function and looking at the dimensions of the n array:

```
dim(sim@n)
## [1] 10 12 100
```

To pull out the abundances of a particular species through time at size you can subset the array. For example to look at Cod through time you can use:

```
sim@n[,"Cod",]
```

This returns a two-dimensional array: time x size, containing the cod abundances. The time dimension depends on the value of the argument t_save when project() was run. You can see that even though we specified dt to be 0.1 when we called project(), the t_save argument had means that the output is only saved every time step.

The n_pp slot can be accessed in the same way.

10.2 Summary methods for *MizerSim* objects

As well as the summary() methods that are available for both *MizerParams* and *MizerSim* objects, there are some useful summary methods to pull information out of a *MizerSim* object (see Table 4). All of these methods have help files to explain how they are used. (It is also possible to use most of these methods with a *MizerParams* object if you also supply the population abundance as an argument. This can be useful for exploring how changes in parameter value or abundance can affect summary statistics and indicators. We won't explore this here but you can see their help files for more details.)

The methods getBiomass() and getN() have additional arguments that allow the user to set the size range over which to calculate the summary statistic. This is done by passing in a combination of the arguments min_l, min_w, max_l and max_w for the minimum and maximum length or weight.

If min_l is specified there is no need to specify min_w and so on. However, if a length is specified (minimum or maximum) then it is necessary for the species parameter data.frame (see Section 8.2) to include the parameters a and b for length-weight conversion. It is possible to mix length and weight constraints, e.g. by supplying a minimum weight and a maximum length. The default values are the minimum and maximum weights of the spectrum, i.e. the full range of the size spectrum is used.

10.2.1 Examples of using the summary methods

Here we show a simple demonstration of using a summary method using the sim object we created earlier. Here, we use getSSB() to calculate the SSB of each species through time (note the use of the head() function to only display the first few rows).

```
ssb <- getSSB(sim)</pre>
dim(ssb)
## [1] 10 12
head(ssb)
##
       gp
## time
                           Sandeel
                                                                        Dab
               Sprat
                                          N.pout
                                                      Herring
            36029938 5.472992e+07
                                        35571252 2.990330e+07
##
      1
                                                                  38479325
##
      2
           177009866 2.430069e+10
                                      4377323145 1.965994e+08
##
      3
         11097299999 4.804739e+11 265729744953 2.428886e+10 13228260702
         87560006143 1.083163e+12 379299271628 1.978630e+11 39036109165
##
      5 351265713190 1.468707e+12 374498905229 6.689569e+11 55641581646
```

```
6 448897618861 1.489816e+12 273063416658 1.169533e+12 52156542433
##
##
##
  time
             Whiting
                             Sole
                                     Gurnard
                                                 Plaice
                                                             Haddock
                                                                              Cod
##
            29928416
                         29191048
                                    34484711
                                               25984507
                                                            25961161
                                                                        20055185
      1
##
      2
            14091030
                         13739444
                                    16293490
                                               10092378
                                                            15575659
                                                                         7626973
                        147257604
##
      3
           563996697
                                   261168563
                                                4561258
                                                         1177016873
                                                                          3715821
##
      4
          5050394382
                      3367749582 1852502768
                                                4207003 15549083633
                                                                        28086231
##
         38424324147 19220173163 3069832259
                                               45016372 43153790789
                                                                      3948533926
##
      6 117652804933 46520219197 3030919441 211853466 80182360951 53439339893
##
       sp
##
          Saithe
  time
##
      1 21521377
##
      2 8169171
##
      3
        3579942
         2716818
##
      4
         4416665
##
      5
##
      6 33596280
```

As mentioned above, we can specify the size range for the getBiomass() and getN() methods. For example, here we calculate the total biomass of each species but only include individuals that are larger than 10 g and smaller than 1000 g.

```
biomass <- getBiomass(sim, min_w = 10, max_w = 1000)
head(biomass)
##
       SD
##
   time
               Sprat
                           Sandeel
                                         N.pout
                                                      Herring
                                                                        Dab
##
      1
            49041758 5.654440e+07
                                       51582276 4.931529e+07
                                                                  51017971
##
      2
           490779088 3.721918e+09
                                   25999573964 1.952166e+10
                                                                 5240583260
##
      3
         25783850174 2.377446e+11 581015555516 3.086905e+11
                                                               55404975864
      4 186375227047 9.017899e+11 549591259535 1.366428e+12 100965688745
##
##
      5 662355802154 1.403032e+12 526356288182 3.311079e+12 113391969285
##
      6 718764900806 1.478552e+12 369262268192 3.608094e+12
##
       sp
##
                              Sole
   time
             Whiting
                                       Gurnard
                                                    Plaice
                                                                Haddock
##
            34694997
                          41533451
                                      46484086
                                                               10470857
                                                  12489697
      1
##
      2
           500106124
                         735729465
                                     303592284
                                                   8919217
                                                             5152082008
                                   7192092253
##
      3
          6737301137
                      19574964756
                                                188000256
                                                            46783953949
##
         30614329729
                      76124227629 11590109862 1039980660 116331943624
##
      5 179933503465 191006534379 13979237136 2231031403 275529691865
      6 294995192308 313047042276 16680463810 2867229959 439216232650
##
##
## time
                 Cod
                         Saithe
##
      1 6.853965e+05
                         1801217
##
      2 1.758179e+06
                         2850771
      3 4.463547e+07
##
                         5245032
                        68143228
##
      4 3.078709e+09
##
      5 3.809203e+10
                      633270381
##
      6 1.062645e+11 2375934419
```

10.3 Methods for calculating indicators

Methods are available to calculate a range of indicators from a *MizerSim* object after a projection. These can be seen in Table 5. You can read the help pages for each of the methods for full instructions on how to use them, along with examples.

With all of the methods in the table it is possible to specify the size range of the community to be used in the calculation (e.g. to exclude very small or very large individuals) so that the calculated metrics can be compared to empirical data. This is used in the same way that we saw with the method getBiomass() in Section 10.2. It is also possible to specify which species to include in the calculation. See the help files for more details.

10.3.1 Examples of calculating indicators

For these examples we use the sim object we created earlier.

The slope of the community can be calculated using the getCommunitySlope() method. Initially we include all species and all sizes in the calculation (only the first five rows are shown):

```
slope <- getCommunitySlope(sim)
head(slope)

## slope intercept r2
## 1 -0.4970061 14.32058 0.7198141
## 2 -1.3011668 21.06361 0.8257857
## 3 -1.4159126 22.74646 0.7787319
## 4 -1.3675689 23.36632 0.7380701
## 5 -1.1725300 23.93529 0.6890267
## 6 -1.0015954 24.25681 0.6612782</pre>
```

This gives the slope, intercept and R^2 value through time (see the help file for getCommunitySlope for more details).

We can include only the species we want with the **species** argument. Here we only include demersal species. We also restrict the size range of the community that is used in the calculation to between 10 g and 5 kg. The **species** is a character vector of the names of the species that we want to include in the calculation.

10.4 Plotting the results

R is very powerful when it comes to exploring data through plots. A useful package for plotting is ggplot2 uses data.frames for input data. Many of the summary methods and slots of the mizer classes are arrays or matrices. Fortunately it is straightforward to turn arrays and matrices into data.frames using the command melt which is in the reshape2 package. Although mizer does include some dedicated plots, it is definitely worth your time getting to grips with these ggplot2 and other plotting packages. This will make it possible for you to make your own plots.

Included in mizer are several dedicated plots that use *MizerSim* objects as inputs (see Table 6). As well as displaying the plots, these methods all return objects of type *ggplot* from the ggplot2 package meaning that they can be further modified by the user (e.g. by changing the plotting theme). See the help page of the individual plot methods for more details. The generic plot() method has also been overloaded for *MizerSim* objects. This produces several plots in the same window to provide a snapshot of the results of the simulation.

Some of the plots plot values by size (for example plotFeedingLevel() and plotSpectra()). For these plots, the default is to use the data at the final time step of the projection. With these plotting methods, it is also possible to specify a different time step or a time range to average the values over before plotting.

10.4.1 Plotting examples

Using the plotting methods is straightforward. For example, to plot the total biomass of each species against time you use the plotBiomass() method:

```
plotBiomass(sim)
```

As mentioned above, some of the plot methods plot values against size at a point in time (or averaged over a time period). For these plots it is possible to specify the time step to plot, or the time period to average the values over. The default is to use the final time step. Here we plot the abundance spectra (biomass), averaged over time = 5 to 10 (see Figure 18):

```
plotSpectra(sim, time_range = 5:10, biomass=TRUE)
```

As mentioned above, and as we have seen several times in this vignette, the generic plot() method has also been overloaded. This produces 5 plots in the same window (plotFeedingLevel(), plotBiomass(), plotM2(), plotFMort() and plotSpectra(), see Figure 19). It is possible to pass in the same arguments that these individual plots use, e.g. arguments to change the time period over which the data is averaged.

```
plot(sim)
```

11 A multispecies model of the North Sea

In this section we try to pull everything together with an extended example of a multispecies model for the North Sea. First we will set up the model, project it through time using historical levels of fishing effort, and then examine the results. We then run two different future projection scenarios. This example is based on the multispecies model in Blanchard et al. (2014).

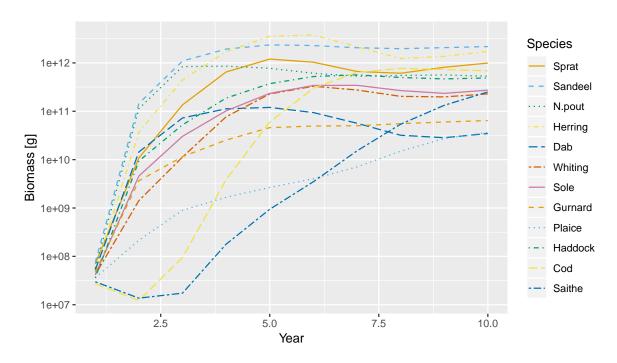


Figure 17: An example of using the plotBiomass() method.

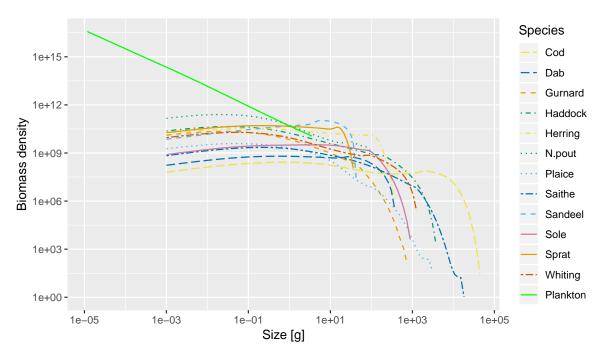


Figure 18: An example of using the plotSpectra() method, plotting values averaged over the period t = 5 to 10.

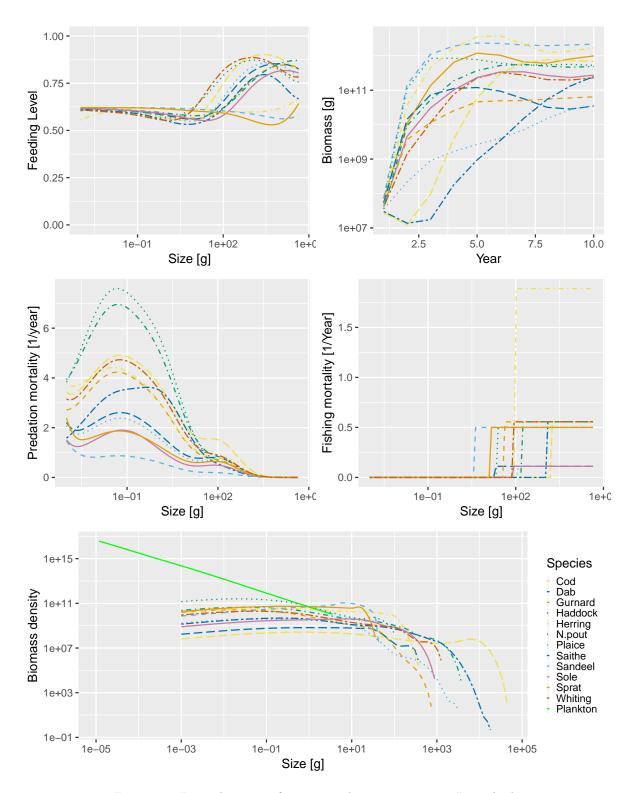


Figure 19: Example output from using the summary plot() method.

11.1 Setting up the North Sea model

The first job is to set up the *MizerParams* object for the North Sea model. In the previous multispecies examples we have already been using the life-history parameters and the interaction matrix for the North Sea model used in Blanchard et al. (2014). We will use them again here but will make some changes. In particular we set up the fishing gears differently.

The parameters and the interaction matrix are stored as *.csv files that need to be read in. We can use the system.file() function to tell us the location of the files. Remember that we need to convert the interaction file into a matrix, hence the use of the as() function.

```
params_location <- system.file("doc/NS_species_params.csv",package="mizer")
params_data <- read.csv(params_location)
inter_location <- system.file("doc/inter.csv",package="mizer")
inter <- as(read.csv(inter_location, row.names=1),"matrix")</pre>
```

The species in the model are Sprat, Sandeel, N.pout, Herring, Dab, Whiting, Sole, Gurnard, Plaice, Haddock, Cod, Saithe which account for about 90% of the total biomass of all species sampled by research trawl surveys in the North Sea. The params_data object is a data.frame with columns for species, w_inf, w_mat, beta, sigma, r_max and k_vb. We have seen before that only having these columns in the species data.frame is sufficient to make a *MizerParams* object. Any missing columns will be added by the default values and relationships in the *MizerParams* constructor. For example, the data.frame does not include columns for h or gamma. This means that they will be estimated using the k_vb column (see Section 8.2).

We will use the default stock-recruitment relationship, which is the Beverton-Holt shape. As we saw in Section 8.4, this requires a column r_max in the species data.frame which contains the maximum recruitment flux for each species. This column is already in the params_data data.frame. The values for r_max are taken from Blanchard et al. (2014). The values were found through a calibration process which is not covered here but will be added to a later version of this manual.

At the moment, the species data.frame does not contain any information on the selectivity of the species. By default, the selectivity function is a knife-edge which only takes a single argument, knife_edge_size. In this model we want the selectivity pattern to be a sigmoid shape which more accurately reflects the selectivity pattern of trawlers in the North Sea. The sigmoid selectivity function is expressed in terms of length rather than weight and uses the parameters 125 and 150, which are the lengths at which 25% and 50% of the stock is selected. The length based sigmoid selectivity looks like:

$$S_l = \frac{1}{1 + \exp(S1 - S2\ l)} \tag{11.1}$$

where l is the length of an individual, S_l is the selectivity at length, $S_l = \log(3)/(l50 - l25)$ and $S_l = l50 \cdot S_l$.

This selectivity function is included in mizer as sigmoid_length(). You can see the help page for more details. As well as the arguments 125 and 150, this function has the arguments a and b to convert between length and weight: $w = al^b$. This is because the sigmoid selectivity function is defined in terms of length, and the size spectrum model works in terms of weight. As explained in Section 8.3, all arguments of the selectivity function need to be in the species parameter data frame. Therefore, columns for 125, 150, a and b need to be added to params_data. We also add a column specifying the name of the selectivity function we wish to use. The data is taken from Blanchard et al. (2014). Note it would probably be easier to add this data directly to the *.csv file and then read it in rather than type it in by hand like we do here:

Note that we do not set up a gear column to give specific gear names. This means that each species will be caught by a separate gear named after the species.

In this model we are interested in projecting forward using historical fishing mortalities. The historical fishing mortality from 1967 to 2010 for each species is stored in the csv file NS_f_history.csv included in the package. As before, we can use read.csv() to read in the data. This reads the data in as a data.frame. We want this to be a matrix so we use the as() function:

```
f_location <- system.file("doc/NS_f_history.csv",package="mizer")
f_history <- as(read.csv(f_location, row.names=1), "matrix")</pre>
```

We can take a look at the first years of the data:

```
head(f_history)
##
        Sprat Sandeel N.pout
                                Herring
                                                Dab
                                                      Whiting
                                                                    Sole Gurnard
## 1967
                     0
                            0 1.0360279 0.09417655 0.8294528 0.6502019
                                                                               0
## 1968
            0
                            0 1.7344576 0.07376065 0.8008995 0.7831250
                                                                               0
                     0
## 1969
            0
                     0
                            0 1.4345001 0.07573638 1.3168280 0.8744095
                                                                               0
## 1970
            0
                            0 1.4342405 0.10537236 1.3473505 0.6389915
                                                                               0
                     \cap
                                                                               0
## 1971
            0
                     0
                            0 1.8234973 0.08385884 0.9741884 0.8167561
## 1972
            0
                     0
                            0 0.9033768 0.09044461 1.3148588 0.7382834
                                                                               0
##
           Plaice
                     Haddock
                                           Saithe
## 1967 0.4708827 0.7428694 0.6677456 0.4725102
  1968 0.3688033 0.7084553 0.6994389 0.4270201
  1969 0.3786819 1.3302821 0.6917888 0.3844648
## 1970 0.5268618 1.3670695 0.7070891 0.5987086
## 1971 0.4192942 0.9173131 0.7737543 0.4827822
## 1972 0.4522231 1.3279087 0.8393267 0.5796321
```

As mentioned in Section 8.3, fishing mortality is calculated as the product of selectivity, catchability and fishing effort (see Equation 8.3). The values in f_history are absolute levels of fishing mortality. We have seen that the fishing mortality in the mizer simulations is driven by the fishing effort argument passed to the project() function. Therefore if we want to project forward with historical fishing levels, we need to provide project() with effort values that will result in these historical fishing mortality levels.

One of the model parameters that we have not really considered so far is **catchability**. Catchability is a scalar parameter used to modify the fishing mortality at size given the selectivity at size and effort of the fishing gear. By default catchability has a value of 1, meaning that an effort of 1 results in a fishing mortality of 1 for a fully selected species. When considering the historical fishing mortality,

one option is therefore to leave catchability at 1 for each species and then use the f_history matrix as the fishing effort. However, an alternative method is to use the effort relative to a chosen reference year. This can make the effort levels used in the model more meaningful. Here we use the year 1990 as the reference year. If we set the catchability of each species to be the same as the fishing mortality in 1990 then an effort of 1 in 1990 will result in the fishing mortality being what it was in 1990. The effort in the other years will be relative to the effort in 1990.

The catchability can be set by including a catchability column in the species parameters data.frame. Doing this overwrites the default values when the *MizerParams* constructor is called.

```
params_data$catchability <- as.numeric(f_history["1990",])</pre>
```

Considering the other model parameters, we will use default values for all of the other parameters apart from kappa, the carrying capacity of the resource spectrum (see Section 3.9). This was estimated along with the values r_max as part of the calibration process described in Blanchard et al. (2014).

We now have all the information we need to create the MizerParams object using the species parameters data.frame.

```
params <- MizerParams(params_data, inter, kappa = 9.27e10)</pre>
```

11.2 Setting up and running the simulation

As we set our catchability to be the level of fishing mortality in 1990, before we can run the projection we need to rescale the effort matrix to get a matrix of efforts relative to 1990. To do this we want to rescale the f-history object to 1990 so that the relative fishing effort in 1990 = 1. This is done using R function sweep(). We then check a few rows of the effort matrix to check this has happened:

```
relative_effort <- sweep(f_history,2,f_history["1990",],"/")</pre>
relative_effort[as.character(1988:1992),]
           Sprat
                   Sandeel
                              N.pout Herring
                                                   Dab
                                                         Whiting
  1988 0.8953804 1.2633229 0.8953804 1.214900 1.176678 0.9972560 1.2786517
##
  1989 1.1046196 1.2931034 1.1046196 1.232790 1.074205 0.8797926 0.9910112
  1990 1.0000000 1.0000000 1.0000000 1.000000 1.000000 1.0000000
  1991 1.1902174 0.8814002 1.1902174 1.108016 1.143110 0.8096927 1.0044944
  1992 1.2500000 0.8500522 1.2500000 1.316576 1.113074 0.7718676 0.9505618
##
         Gurnard
                   Plaice
                            Haddock
                                         Cod
                                                Saithe
## 1988 0.0000000 1.176678 0.9946140 1.045964 1.0330579
  1989 0.0000000 1.074205 0.8545781 1.060538 1.1223140
  1990 1.0000000 1.000000 1.0000000 1.000000
  1991 0.8096927 1.143110 0.7971275 1.001121 0.9619835
  1992 0.7718676 1.113074 0.8797127 0.970852 1.0528926
```

We could just project forward with these relative efforts. However, the population dynamics in the early years will be strongly determined by the initial population abundances (known as the transient behaviour - essentially the initial behaviour before the long term dynamics are reached). As this is ecology, we don't know what the initial abundance are. One way around this is to project forward at a constant fishing mortality equal to the mortality in the first historical year until equilibrium is reached. We then can carry on projecting forward using the remaining years of effort. This approach reduces the impact of transient dynamics.

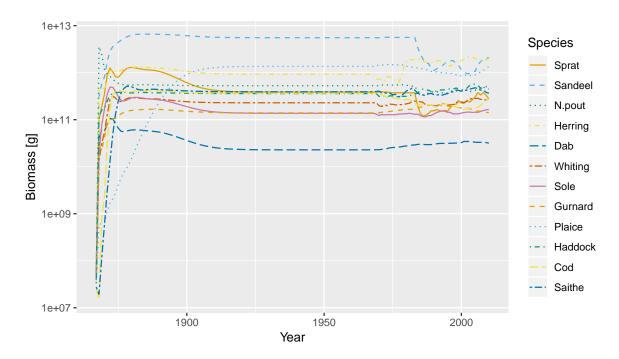


Figure 20: Simulated biomasses of stocks in the North Sea with 100 years of transients.

Here we make an initial effort matrix of 100 years at the first effort level. We need to include dimension names for the time dimension. We then stick it on top of the original matrix of historical relative effort using rbind().

We now have our parameter object and out matrix of efforts relative to 1990. This includes an initial 100 years of constant relative effort at the 1957 level, followed by the relative effort from 1957 to 2010. We use this effort matrix as the effort argument to the project() method. We use dt = 0.5 (the simulation will run faster than with the default value of 0.1, but tests show that the results are still stable) and save the results every year.

```
sim <- project(params, effort=relative_effort, dt = 0.5, t_save = 1)</pre>
```

Plotting the results, we can see how the biomasses of the stocks change over time (Figure 20). You can see the 100 year period of transients with constant fishing fishing mortality before the historical relative mortality is used from 1967.

```
plotBiomass(sim)
```

To explore the state of the community it is useful to calculate indicators of the unexploited community. Therefore we also project forward for 100 years with 0 fishing effort.

```
sim0 <- project(params, effort=0, dt = 0.5, t_save = 1, t_max = 100)</pre>
```

11.3 Exploring the model outputs

Here we look at some of the ways the results of the simulation can be explored. We calculate the community indicators "mean maximum weight", "mean individual weight", "community slope" and the "large fish indicator" (LFI) over the simulation period, and compare them to the unexploited values. We also compare the simulated values of the LFI to a community target based on achieving a high proportion of the unexploited value of the LFI of $0.8LFI_{F=0}$ (Rochet et al., 2011).

The indicators are calculated using the methods described in see Table 5 and Section 10.2. Here we calculate the LFI and the other community indicators for the unexploited community. As in Blanchard et al. (2014), when calculating these indicators we only include demersal species and individuals in the size range 10 g to 100 kg, and the LFI is based on species larger than 40 cm. Each of these methods returns a time series. We are interested only in the equilibrium unexploited values so we just select the final time step (year = 100).

We also calculate the time series of these indicators for the exploited community (we are only interested in the fishing history years, 1967 to 2010, ignoring the transients):

```
years <- 1967:2010
lfi <- getProportionOfLargeFish(sim, species = demersal_species,
    min_w = 10, max_w = 100e3, threshold_l = 40)[as.character(years)]
mw <- getMeanWeight(sim, species = demersal_species,
    min_w = 10, max_w = 100e3)[as.character(years)]
mmw <- getMeanMaxWeight(sim, species = demersal_species,
    min_w = 10, max_w = 100e3)[as.character(years), "mmw_biomass"]
slope <- getCommunitySlope(sim, species = demersal_species,
    min_w = 10, max_w = 100e3)[as.character(years), "slope"]</pre>
```

We can plot the exploited and unexploited indicators, along LFI reference level. Here we do it using ggplot2 which uses data.frames We make three data.frames (one for the time series, one for the unexploited levels and one for the reference level): Each data.frame is a data.frame of each of the measures, stacked on top of each other.

```
library(ggplot2)
# Simulated data
community_plot_data <- rbind(</pre>
```

```
data.frame(year = years, measure = "LFI", data = lfi),
    data.frame(year = years, measure = "Mean Weight", data = mw),
    data.frame(year = years, measure = "Mean Max Weight", data = mmw),
    data.frame(year = years, measure = "Slope", data = slope))
# Unexploited data
community_unfished_data <- rbind(</pre>
    data.frame(year = years, measure = "LFI", data = lfi0[[1]]),
    data.frame(year = years, measure = "Mean Weight", data = mw0[[1]]),
    data.frame(year = years, measure = "Mean Max Weight", data = mmw0[[1]]),
    data.frame(year = years, measure = "Slope", data = slope0[[1]]))
# Reference level
community_reference_level <-</pre>
    data.frame(year=years, measure = "LFI", data = lfi0[[1]] * 0.8)
# Build up the plot
p <- ggplot(community_plot_data) + geom_line(aes(x=year, y = data)) +</pre>
    facet_wrap(~measure, scales="free")
p <- p + geom_line(aes(x=year,y=data), linetype="dashed",</pre>
    data = community_unfished_data)
p + geom_line(aes(x=year,y=data), linetype="dotted",
    data = community_reference_level)
```

According to our simulations, historically the LFI in the North Sea has been below the reference level.

11.4 Future projections

As well as investigating the historical simulations, we can run projections into the future. Here we run two projections to 2050 with different fishing scenarios.

- 1. Continue fishing at 2010 levels (the status quo scenario).
- 2. From 2010 to 2015 linearly change the fishing mortality to approach F_{MSY} and then continue at F_{MSY} until 2050.

Rather than looking at community indicators here, we will calculate the SSB of each species in the model and compare the projected levels to a biodiversity target based on the reference point $0.1SSB_{F=0}$ (Rochet et al., 2011). The F_{MSY} values are also taken from Rochet et al. (2011).

Before we can run the simulations, we need to set up arrays of future effort. We will continue to use effort relative to the level in 1990. Here we build on our existing array of relative effort to make an array for the first scenario. Note the use of the t() command to transpose the array. This is needed because R recycles by rows, so we need to build the array with the dimensions rotated to start with. We make an array of the future effort, and then bind it underneath the relative_effort array used in the previous section.

The relative effort array for the second scenario is more complicated to make and requires a little bit of R gymnastics (it might be easier for you to prepare this in a spreadsheet and read it in). For this one we need values of F_{MSY} .

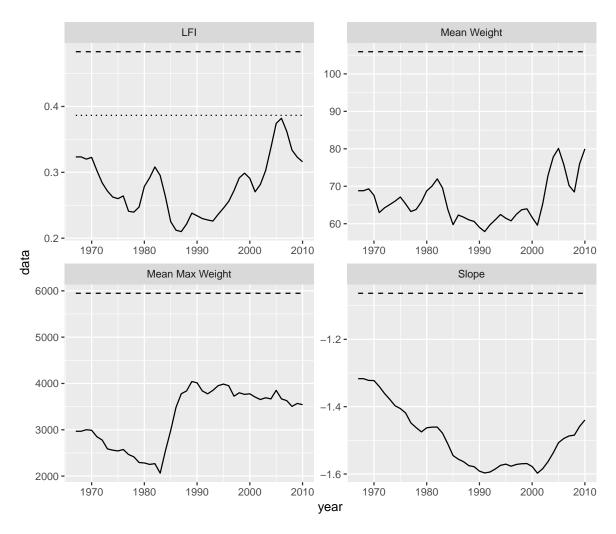


Figure 21: Historical (solid) and unexploited (dashed) and reference (dotted) community indicators for the North Sea multispecies model.

Both of our new effort scenarios still include 100 years at the 1967 level to reduce the impact of the transient behaviour. We are now ready to project the two scenarios.

```
sim1 <- project(params, effort = scenario1, dt = 0.5, t_save = 1)
sim2 <- project(params, effort = scenario2, dt = 0.5, t_save = 1)</pre>
```

We can now compare the projected SSB values in both scenarios to the biodiversity reference points. First we calculate the biodiversity reference points (from the final time step in the unexploited sim0 simulation):

```
ssb0 <- getSSB(sim0)["100",]
```

Now we build a data frame of the projected SSB for each species, ignoring the transients. We make use of the melt() function in the very useful reshape2 package (REF).

```
library(reshape2)
years <- 1967:2050
ssb1 <- getSSB(sim1)[as.character(years),]</pre>
ssb2 <- getSSB(sim2)[as.character(years),]</pre>
ssb1_df <- melt(ssb1)
ssb2_df <- melt(ssb2)
ssb_df <- rbind(</pre>
    cbind(ssb1_df, scenario = "Scenario 1"),
    cbind(ssb2_df, scenario = "Scenario 2"))
ssb_unexploited_df <- cbind(expand.grid(</pre>
    sp = names(ssb0),
    time = 1967:2050),
    value = as.numeric(ssb0),
    scenario = "Unexploited")
ssb_reference_df <- cbind(expand.grid(</pre>
    sp = names(ssb0),
    time = 1967:2050),
    value = as.numeric(ssb0*0.1),
    scenario = "Reference")
ssb_all_df <- rbind(
    ssb_df,
    ssb_unexploited_df,
    ssb_reference_df)
p <- ggplot(ssb_all_df) +</pre>
```

```
geom_line(aes(x = time, y = value, colour = scenario)) +
  facet_wrap(~sp, scales = "free", nrow = 4)
p + theme(legend.position = "none")
```

12 Scale-invariant, trait-based model

12.1 Introduction

Constructing models that allow fish species to coexist is not trivial. This applies as much to size-spectrum models that use the mizer software tool, as it does to other kinds of multispecies models. Current size-spectrum models achieve coexistence by assuming that stock-recruitment relationships are strong enough within species to promote coexistance of the species. They do this by making the controlling parameter $R_{max.i}$ in Equation 3.12 sufficiently small. Although coexistence can be achieved in this way, it can necessitate rather small values of $R_{max.i}$, with major effects on persistence and stability of species.

This and the next Section 13 provide an alternative way of generating sets of coexisting species, without the need for such strong stock-recruitment relationships. This makes stocks more sensitive to changes in the environment, such as those caused by fishing. To motivate the new approach, Figure 23 compares it with the trait-based model in Section 6 in the presence of a substantial amount of fishing. In the case of the trait-based model, all species persist under fishing (Figure 23.1). In this instance, the species with largest maximum weight enters the fishery at about half of its weight at maturation, and persists because its stock-recruitment relationship is sufficiently strong to boost its rate of increase when rare. You can construct Figure 23.1, using the following code:

The approach developed below allows the stock-recruitment relationship to be weakened or completely removed, with the result that species are more sensitive to fishing (Figure 23.2). In the example shown, fishing drives the largest and most vulnerable species to extinction (there is no stock-recruitment relationship in this instance). Some density-dependent feedbacks still remain, but they emerge from the internal dynamics Rossberg et al. (2013). You can construct Figure 23.2, using the following code:



Figure 22: Historical and projected SSB under two fishing scenarios. Status quo (red), Fmsy (yellow). Unexploited (blue) and reference levels (purple) are also shown.

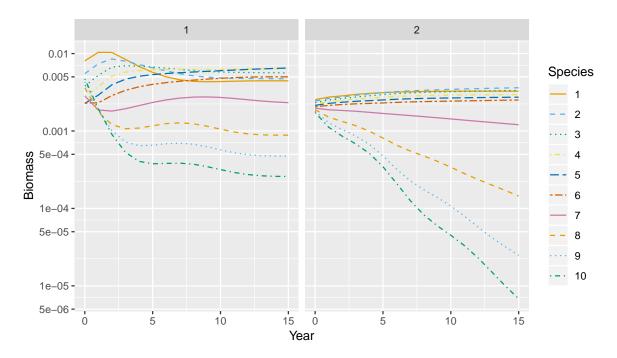


Figure 23: Biomass plots following introduction of fishing (1) in the trait-based model from Section 6, and (2) in the scale-invariant model developed here. There are ten species; W is taken over a range 10 g to 1000 g, uniformly spaced on the log-scaled mass axis. The initial state is close to the steady state in the absence of fishing. Recruitment to the multispecies fishery is knife-edge at 100 g and fishing mortality rate is set at $F = 1 \text{ yr}^{-1}$.

The key for constructing these models is a special power-law relationship between body weight and density, which marine ecosystems are often observed to be near, after aggregating over species Sheldon et al. (1972). The significance of the power law is that, in its neighbourhood, coexistence of species becomes easier to achieve. In fact, on the exact power-law, it has been proved that an infinite number of species coexist in a unicellular plankton model Cuesta et al. (2018). Related numerical simulations using finite number of species support the proposition that coexistence of multiple species is easier to achieve near the power law Law et al. (2016). These properties readily extend to multicellular fish assemblages (Southwell, Delius unpublished results).

We build the alternative approach here in two steps. First, this section describes a background spectrum designed to bring the trait-based model (see Section 6) close to a scale-invariant form (see Section 14), for which the steady-state is known analytically (Equation 14.1). For want of a better term, we call this model the *scale-invariant*, trait-based model, with the caveat that the model is close to, but not exactly, scale invariant.

Second, in the following Section 13, these background species are replaced by foreground species with specified properties in a fish assemblage.

12.2 Scale invariance

Dynamical systems with scale-invariant properties are not standard currency in ecology, and this subsection can be skipped. However the approach is underpinned by scale invariance with respect to body weight, so we briefly introduce some key concepts here. There is little more in this than allometric scalings of ecological rates with respect to body weight, for the most part familiar and widely documented in ecology.

What is scale invariance? Consider a species with some characteristic weight (maximum weight W will do for the purpose), and with a density function N(w,t) that has dynamics given by the size-spectrum model (Equation 3.1). Consider a second species with maximum weight cW, where c is a positive rescaling factor. Then Equation 3.1 would be scale-invariant, if the latter species had dynamics the same as the first when rescaled as $c^{\lambda+1}N(cw,c^{1-n}t)$, for any c>0. Here λ is the exponent of the resource spectrum, and n is the exponent for maximum food intake.

This rather delphic statement basically says that, under scale invariance, knowing the dynamics of one species is enough to know the dynamics of every species. Strictly speaking, it could only apply to Equation 3.1 if there was a continuum of maximum weights, with a species at every W>0. Clearly, this cannot be the case in a multispecies spectrum with a finite set of species, because the Ws are typically separated by finite intervals, and the spectrum has fixed lower and upper boundaries, outside which there are no species. Therefore, a scale-invariant system is, at best, an idealisation of a size-spectrum model with a finite number of species.

Why bother with scale invariance? There is an ecological reason and a mathematical one. The ecological reason is that, in marine ecosystems, abundance (aggregated over species) as a function of body mass, is often observed to be quite close to a power law Sheldon et al. (1972). The existence of this remarkable regularity, plus the fact that it promotes coexistence of species, supports the development of scale-invariant models.

The mathematical reason is that scale-invariant systems possess symmetries which make them easier to understand. For instance, the assumption of scale invariance in the system with a continuum of maximum weights allows an exact analytic expression for a steady state of the system to be derived. Although scale invariance cannot be met exactly in the system with a finite number of species, it can still guide the choice of parameter values that are likely to permit coexistence of species.

Note that we are not suggesting that real assemblages of fish species are at rest on an exact power-law. Rather we use scale invariance to construct background assemblages that facilitate coexistence of

observed fish species (foreground species), without calling for strong stock-recruitment relationships.

12.3 Implementing the scale-invariant model

Here we describe how to run the scale-invariant model, and make some comparisons with the trait-based model in Section 6.

To help set up a scale invariant trait-based model, there is a wrapper function, set_scaling_model(). Like the set_community_model() and set_tait_model() functions described above, this function can take many arguments. Most of them have default values so you don't need to worry about them for the moment. Now let us give an example of how to setup the scale-invariant trait-based model:

The main parameters of interest are the number of the species in the model (no_sp), the minimum egg size the minimum maturity size of a species and the minimum and maximum asymptotic sizes and (max_w_inf) respectively. The egg, maturity and asymptotic sizes are spread evenly on a logarithmic scale. The Beverton-Holt stock recruitment relationship is turned off by default.

Once a *MizerParams* object has been created for the scale-invariant model, it can be run in the usual way:

```
sim <- project(params, t_max=5, effort = 0)</pre>
```

We make a plot of the biomass over time (Figure 24) as follows:

```
plotBiomass(sim)
```

One can see from Figure 24 that the system is initiated very close to a steady state, and it is further attracted to the steady state without the need to impose any stock recruitment relationship (at least under default settings).

We can check that the steady state lies close to a power law by plotting the biomass densities of the different species, as well as their total, which evidently is close to the power law (Figure 25).

```
plotSpectra(sim, total = TRUE)
```

12.4 Details of changes to the trait-based model

Here we document the changes made to the Mizer software tool described in Section 3, in order to generate species assemblages close to scale invariance. The new model is similar to the original trait-based model of Section 6, but includes some modifications and restrictions to get assemblages that are close to scale invariance. The changes are as follows.

• For the model to be scale invariant, the exponent of metabolic intake n needs to be equal to the exponent p of metabolic loss.

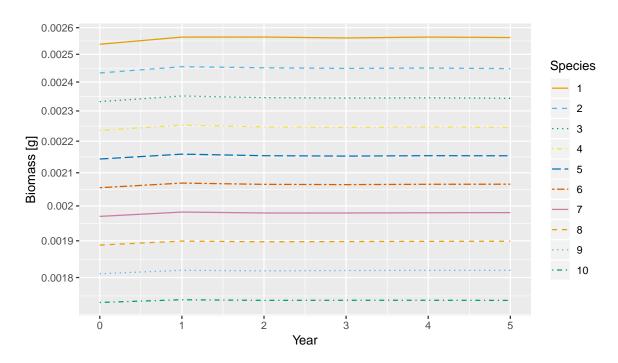


Figure 24: A plot of time vs biomass for the scale invariant trait-based model with no fishing.

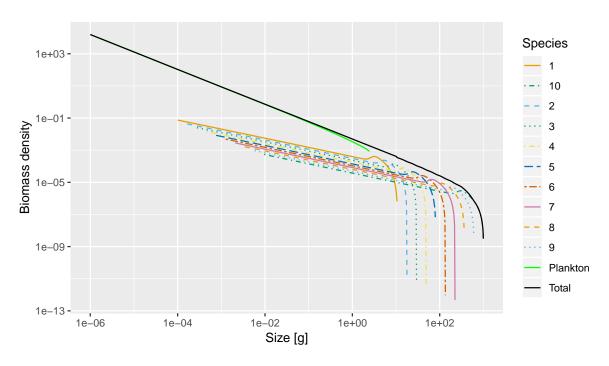


Figure 25: A plot of weight vs biomass density for the steady state of the scale invariant trait-based model with no fishing.

- Scale invariance also requires that the exponent of the resource spectrum λ must satisfy the relation $\lambda = 2 n + q$, where n is the exponent of metabolic intake and q is the exponent of the volumetric search rate.
- (Equation 3.4) Feeding depends on prey body size, but not on prey species identity, so $\theta_{ij} = 1$ for all i, j. Note however that the feeding preference function $\phi_i(w_p/w)$ already has scale invariance built into it, because predation depends on the ratio of prey to predator weight. Thus no modification to growth and mortality caused by predation is needed in moving to scale invariance.
- (Equation 3.8) We assume that the proportion of energy allocated to reproduction $\psi_i(w)$ is given by the step-like function

$$\psi_i(w) = \begin{cases} 0 & \text{if } w < w_{*,i} \\ \left(\frac{w}{W_i}\right)^{1-n} & \text{otherwise} \end{cases}$$
 (12.1)

This can be achieved by taking the form given by Equation 3.8, and letting $u \to \infty$. This is not a requirement for scale invariance; the assumption was made for the mathematical reason that it is then possible to get a closed-form expression for the steady state.

- (Equation 3.11) Scale invariance requires egg weight to be a fixed fraction of maximum weight. It is therefore indexed by species $w_{0,i}$, rather than taking a single size w_0 . Egg size does vary over about two orders of magnitude in teleosts, but there is evidence that at least the larger teleosts are unusual in marine systems in lacking a scaling relationship between egg wight and adult weight Andersen et al. (2016). Scale invariance of egg weight should therefore be seen as a mathematical restriction required to generate the scale-invariant background assemblage, in so far as the background comprises teleost fish.
- (Equation 3.12) A stock-recruitment relationship is not required to create a steady state in the scale-invariant, trait-based model. However, a stock-recruitment relationship can be included in the scale-invariant trait-based model by setting the value of r_fac. Here r_fac equals the maximum recruitment $R_{max.i}$ divided by the actual recruitment R_i at our steady state. By default the stock-recruitment relationship is turned off, by setting to go to infinity. This has the effect of also making $R_{max.i} \to \infty$, and so Equation 3.12 is effectively replaced with the simple relationship $R_i = R_{p.i}$.
- (Equation 3.14) Beyond the upper limit of body weight. The total mortality needs to scale with body weight. In practice, body weight always has an upper limit in a real ecosystem, and predation mortality goes to zero as this limit is approached. Some compensation is needed for this in the background mortality. Thus, we replace the background mortality in Equation 3.14 with a more intricate expression $\mu_b(w)$ given by Equation 14.4. Essentially this term represents the predation mortality which would be induced by predators beyond the upper limit of body sizes explicitly modelled, under the assumption that the abundance of such predators continue the scale invariant pattern.
- (Equation 3.15) The resource spectrum extends from the smallest weight at which an explicitly modeled fish may eat. We define the carrying capacity $c_p(w)$ of the background resource so when our system is at steady state, the combination of the background resource spectrum and the aggregate abundance of the explicitly modeled species is the power law $\kappa w^{-\lambda}$. An expression for how we set $c_p(w)$ within the scale-invariant trait-based model is given by Equation 14.5.
- By default the scale-invariant trait-based model is initialized at a steady state (Equation 14.1) (provided no fishing is being performed), whereas the original trait based model is not initialized near its steady state.

13 Implementing explicit species in a scale-invariant background

13.1 Introduction

In Section 12 we saw that using strong stock recruitment relationships, as implemented within the models discussed in sections 6 and 11 can lead to scenarios where the stock levels are unrealistically insensitive to changes in the environment. In order to fix this issue we want to create a model where species of interest can co-exist and interact without imposing a strong stock recruitment relationship. The key to our approach is to use species from the scale-invariant trait based model as a type of background or substrate, into which the heterogeneous species of specific interest (the *foreground species*) can added.

We begin with only the scale-invariant background, which is setup close to a steady state by the set_scaling_model() command. We add new species using the addSpecies() command, in such a way that the resulting system remains close to a steady state. To achieve this we lower the abundances of the background species in our candidate steady state to compensate for the addition of the new foreground species, so that the background species still have the same food levels, and growth rates, as they did in the original system. We also choose the abundance curve for the newly added species so that it will be time-invariant under Equation 3.1. Additional steps are taken to fine tune the resulting state to make sure that the background species are close to time-invariant under Equation 3.1, and that the quantity of fish growing up from the egg size is balanced by the rate of egg production.

13.2 Adding a foreground species to a scale-invariant background

Initially, when we start with the scale-invariant trait-based model, these species are organized, so that their aggregate abundance follows a power-law. This can be done using the set_scaling_model() command (discussed in Section 12) as follows:

Let us introduce a species which we are interested in modelling explicitly into this background using our addSpecies() command. For the sake of example we shall introduce a red mullet, we start by specifying its parameters using a dataframe with a single row:

```
species_params <- data.frame(
  species = "Mullet",
  w_min = 0.001,
  w_inf = 173.2425,
  w_mat = 15.14863,
  beta = 283,
  sigma = 1.8,
  z0 = 0,
  alpha = 0.6,</pre>
```

```
erepro = 0.1,
sel_func = "sigmoid_length",
gear = "sigmoid_gear",
125 = 13.17291,
150 = 15.48,
k = 0,
k_vb = 0.6,
a = 0.0085,
b = 3.11,
gamma = 0.0017,
h = 50,
linecolour = "red",
linetype = "solid"
)
```

Foreground species of specific interest can be introduced into our background using the following command:

This code creates a new *MizerParams* object containing the original background species and the new foreground species, mullet. The addSpecies() command attempts to construct a new approximate steady state (params_out@initial_n) including the new species.

The stock recruitment relationship can be controlled by setting the value of r_fac, as described in Subsection 12.4.

We can perform a simulation with our new system, including the mullet, in the usual way:

```
sim <- project(params_bg_m, t_max = 25, effort = 0.4)
```

We can see from the resulting plot of time vs biomass that the system is initiated close to a steady state (Figure 26):

```
plotBiomass(sim)
```

We can also visualize the relative abundances of the different species (Figure 27) with the following command:

```
plotSpectra(sim)
```

13.3 Adding another species

In practical fisheries science one will have several species that one wishes to model explicitly. Further foreground species can be added into our system by repeated use of the addSpecies() command. Let us demonstrate this by adding hake into our system with background and mullet. We start by specifying the data for the hake:

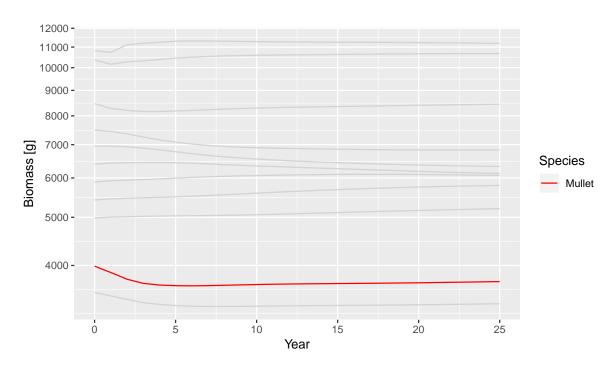


Figure 26: Example plot of time vs biomass for the scale invariant trait-based model plus mullet.

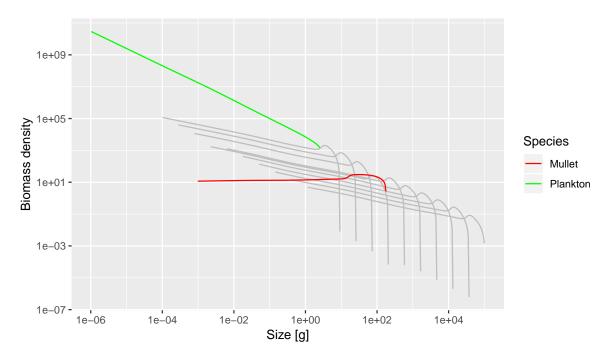


Figure 27: Example plot of weight vs abundance for the scale invariant trait-based model plus mullet, in the final state of our simulation.

```
species_params <- data.frame(</pre>
  species = "Hake",
  w_{min} = 0.001,
  w_{inf} = 4174.194,
  w_mat = 183.5169,
  beta = 11.02318,
  sigma = 1.1,
  z0 = 0,
  alpha = 0.6,
  erepro = 0.1,
  sel_func = "sigmoid_length",
  gear = "sigmoid_gear",
  125 = 16.09244,
  150 = 16.6,
  k = 0,
  k_vb = 0.1,
  a = 0.0046,
  b = 3.12,
  gamma = 0.003,
  h = 20,
  linecolour = "blue",
  linetype = "solid"
```

Now we add the hake into our system:

We visualize the initial condition, close to steady state (Figure 28) using the following command:

```
plotSpectra(params_bg_m_h)
```

To see that this is close to a steady state we shall evolve the system and show how biomass changes over time (Figure 29):

```
sim <- project(params_bg_m_h, t_max = 50, t_save = 5, effort = 0.4)
plotBiomass(sim)</pre>
```

The steady() command can be used to fine tune the initial condition to be very close to a steady state:

```
params_bg_m_h2 <- steady(params_bg_m_h, effort = 0.4)</pre>
```

This results in a configuration very close to a steady state, as we can see by evolving the system and plotting how biomass changes over time (Figure 30):

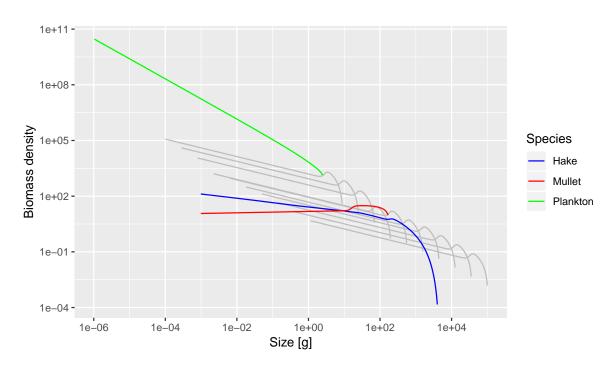


Figure 28: A plot of weight vs biomass density for the near steady state created by adding mullet and hake to a scale-invariant background.

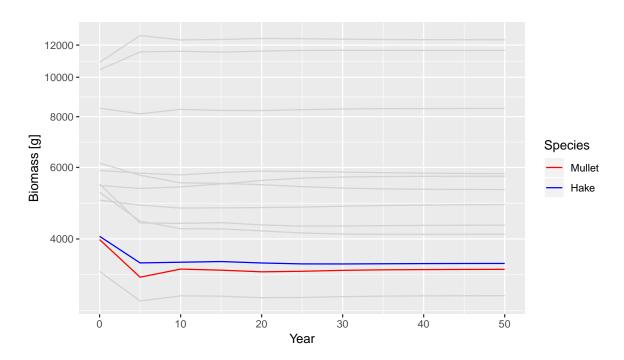


Figure 29: A plot of time vs biomass showing our system with background species, mullet and hake, evolving to a nearby steady state.

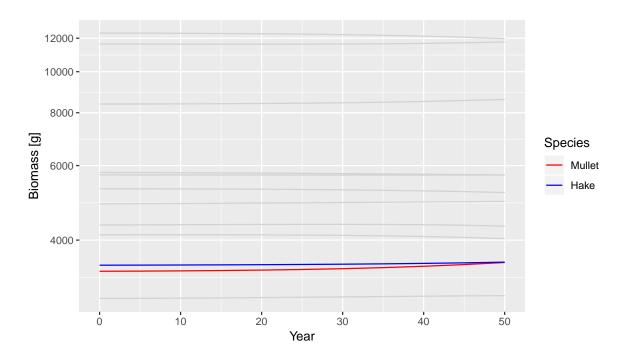


Figure 30: A plot of time vs biomass showing our system with background species, mullet and hake evolving from our fine tuned nearby steady state.

```
sim2 <- project(params_bg_m_h2, t_max = 50, t_save = 5, effort = 0.4)
plotBiomass(sim2)</pre>
```

14 Appendix

In this section we give some of the more technical details behind the scale-invariant model, and how it is implemented in mizer.

14.1 A steady state solution

Assuming scale invariance allows us to find the following exact analytic expression for a steady state. This corresponds to the following form for the abundance within the discrete approximation to the scale-invariant system implemented by mizer:

$$N_i(w,t) = H\left(\frac{w_{0,1}}{w_{0,i}}\right)^{\lambda} \left(\frac{w_{0,i}}{w}\right)^{\mu_0/\hbar} \hbar^{-1} w^{-n} M_i(w)$$
(14.1)

where

$$M_{i}(w) = \begin{cases} 1, & \text{if } w < w_{*i} \\ \frac{1}{\left(1 - \left(\frac{w}{W_{i}}\right)^{1-n}\right)} \left(\frac{1 - \left(\frac{w}{W_{i}}\right)^{1-n}}{1 - \left(\frac{w_{*i}}{W_{i}}\right)^{1-n}}\right)^{\frac{1}{1-n}\left(\frac{\mu_{0}}{\hbar}\right)}, & \text{otherwise} \end{cases}$$
(14.2)

and

$$\mu_0 = (1 - f_0)\sqrt{2\pi}\kappa\gamma\sigma\beta^{n-1}\exp\left(\frac{\sigma^2(n-1)^2}{2}\right). \tag{14.3}$$

As the number of species becomes large we have that $\sum_i N_i(w)$ is approximately proportional to $\kappa w^{-\lambda}$, $\forall w \in [\min\{w_{*i}\}, \max\{w_{*i}\}]$. The constant H is chosen so that $\sum_i N_i(w)$ is approximately equal to $\kappa w^{-\lambda} \ \forall w \in [\min\{w_{*i}\}, \max\{w_{*i}\}]$. This steady state is special because it is invariant under the type of rescaling described above. We also have to choose parameters in such a way that Equation 3.11 holds. However, if it holds for one species, then it holds for all species due to scale-invariance. Although the original trait based model had a similar level of simplicity, and a partial description of something like a steady state was possible, a careful reading of Section 3 of Hartvig et al. (2010) reveals that it was in fact impossible to setup such a system so that the average number of offspring produced over an individuals lifespan is one, for each species, without imposing a stock recruitment relationship. This is part of the reason why stock recruitment relationships were imposed on previous models. However we believe that the stock recruitment relationships should emerge out of the life histories which size spectrum models claim to be able to model, rather than being imposed for outside the model.

14.2 Background mortality in the scale invariant model

We arrived at our expression for $\mu_b(w)$ by considering that in the steady state of continuous scale-invariant trait based model, the total mortality rate of of individuals is given by the power-law $\mu_0 w^{n-1}$. In the finite system in mizer, individuals are only modelled up to a given size, and so we define $\mu_b(w)$ as the difference between the desired power-law mortality rate, and the predation rate exhibited by explicitly modeled species at our steady state:

$$\mu_{b,i}(w) = \max\{\mu_0 w^{n-1} - \mu_{p,i}(w), 0\}$$
(14.4)

where μ_0 is given by Equation 14.3, and $\mu_{p,i}(w)$ is the predation mortality, given by Equation 3.13, where the abundance N is the abundance at our steady state, given by Equation 14.1. This is done so that (provided we choose parameters so $\mu_{b,i}(w) = \mu_0 w^{n-1} - \mu_{p,i}(w) \ge 0$.) we ensure that the total mortality rate on explicitly modeled species is $\mu_0 w^{n-1}$, which scales with weight in the way required for scale invariance.

14.3 Background resources in the scale invariant model

We define the carrying capacity $c_p(w)$ of the background resource so when our system is at steady state, the combination of the background resource spectrum and the aggregate abundance of the explicitly modeled species is the power law $\kappa w^{-\lambda}$. This is achieved choosing the carrying capacity of the background resource to be

$$c_p(w) = \min\left\{ \left(1 + \frac{\mu_p(w)}{r_0 w^{p-1}} \right) \left(\kappa w^{-\lambda} - \sum_i N_i(w) \right), 0 \right\}$$
(14.5)

Note that, much like in the background mortality term, we require that the aggregate abundance $\sum_{i} N_{i}(w)$ is less than or equal to the power law $\kappa w^{-\lambda}$ within the appropriate size range (i.e., for $w \leq \min\{w_{*i}\}$), so that we do not have to use our $\min\{*,0\}$ operation to rewrite negative entries.

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References

- K. H. Andersen and J. E. Beyer. Asymptotic size determines species abundance in the marine size spectrum. *The American Naturalist*, 168(1):54–61, July 2006. ISSN 0003-0147, 1537-5323. doi: 10.1086/504849.
- K. H. Andersen and M. Pedersen. Damped trophic cascades driven by fishing in model marine ecosystems. *Proceedings of the Royal Society B-Biological Sciences*, 277(1682):795–802, March 2010. ISSN 0962-8452. doi: 10.1098/rspb.2009.1512. WOS:000273882800018.
- K. H. Andersen and Jake C. Rice. Direct and indirect community effects of rebuilding plans. *ICES Journal of Marine Science: Journal du Conseil*, 67(9):1980–1988, January 2010. ISSN 1054-3139, 1095-9289. doi: 10.1093/icesjms/fsq035.
- K. H. Andersen, J. E. Beyer, and P. Lundberg. Trophic and individual efficiencies of size-structured communities. *Proceedings of the Royal Society B: Biological Sciences*, 276(1654):109–114, July 2009a. ISSN 0962-8452, 1471-2954. doi: 10.1098/rspb.2008.0951.
- K. H. Andersen, K. D. Farnsworth, M. Pedersen, H. Gislason, and J. E. Beyer. How community ecology links natural mortality, growth, and production of fish populations RID b-5546-2008 RID c-1357-2008. *Ices Journal of Marine Science*, 66(9):1978–1984, October 2009b. ISSN 1054-3139. doi: 10.1093/icesjms/fsp161. WOS:000269611300018.
- K. H. Andersen, T. Berge, R. J. Goncalves, M. Hartvig, J. Heuschele, S. Hylander, N. S. Jacobsen, C. Lindemann, E. A. Martens, A. B. Neuheimer, K. Olsson, A. Palacz, F. Prowe, J. Sainmont, S. J. Traving, A. W. Visser, N. Wadhwa, and Kirboe T. Characteristic sizes of life in the oceans, from bacteria to whales. *Annual Review of Marine Science*, 8:3.1–3.25, 2016.
- K.H. Andersen, J.E. Beyer, M. Pedersen, N.G. Andersen, and H. Gislason. Life-history constraints on the success of the many small eggs reproductive strategy. *Theoretical Population Biology*, 73(4): 490–497, June 2008. ISSN 0040-5809. doi: 10.1016/j.tpb.2008.02.001.
- Knud Peter Andersen and Erik Ursin. A multispecies extension to the Beverton and Holt theory of fishing, with accounts of phosphorus circulation and primary production. *Meddelelser fra Danmarks Fiskeri- og Havundersøgelser*, 1977.
- M. Barange, G. Merino, J. L. Blanchard, J. Scholtens, J. Harle, E. H. Allison, J. I. Allen, J. Holt, and S. Jennings. Impacts of climate change on marine ecosystem production in societies dependent on fisheries. *Nature Clim. Change*, 4(3):211–216, March 2014. ISSN 1758-678X. URL http://dx.doi.org/10.1038/nclimate2119.
- Eric Benoît and Marie-Joëlle Rochet. A continuous model of biomass size spectra governed by predation and the effects of fishing on them. *Journal of Theoretical Biology*, 226(1):9–21, January 2004. ISSN 0022-5193. doi: 10.1016/S0022-5193(03)00290-X.

- Julia L. Blanchard, Simon Jennings, Richard Law, Matthew D. Castle, Paul McCloghrie, Marie-Jolle Rochet, and Eric Benot. How does abundance scale with body size in coupled size-structured food webs? *Journal of Animal Ecology*, 78(1):270280, 2009. ISSN 1365-2656. doi: 10.1111/j.1365-2656. 2008.01466.x.
- Julia L. Blanchard, Ken H. Andersen, Finlay Scott, Niels T. Hintzen, Gerjan Piet, and Simon Jennings. Evaluating targets and trade-offs among fisheries and conservation objectives using a multispecies size spectrum model. *Journal of Applied Ecology*, 2014.
- J. A. Cuesta, G. W. Delius, and R. Law. Sheldon spectrum and the plankton paradox: two sides of the same coina trait-based plankton size-spectrum model. *J. Math. Biol.*, 76:67–96, 2018.
- Samik Datta, Gustav W. Delius, and Richard Law. A jump-growth model for predator-prey dynamics: derivation and application to marine ecosystems. *Bulletin of Mathematical Biology*, 72(6):1361–1382, January 2010. ISSN 0092-8240, 1522-9602. doi: 10.1007/s11538-009-9496-5.
- André M. De Roos and Lennart Persson. Physiologically structured models from versatile technique to ecological theory. *Oikos*, 94(1):5171, 2001. ISSN 1600-0706. doi: 10.1034/j.1600-0706.2001.11313.x.
- Tom Fenchel. Intrinsic rate of natural increase: The relationship with body size. *Oecologia*, 14(4): 317–326, December 1974. ISSN 0029-8549, 1432-1939. doi: 10.1007/BF00384576.
- Martin Hartvig. Food web ecology. Ph.D., Lund University, 2011.
- Martin Hartvig, Ken H. Andersen, and Jan E. Beyer. Food web framework for size-structured populations. arXiv:1004.4138, April 2010. doi: 10.1016/j.jtbi.2010.12.006. Journal of Theoretical Biology, 272(1):113-122, 2011.
- Martin Hartvig, K. H. Andersen, and Jan E. Beyer. Food web framework for size-structured populations RID c-4303-2011. *Journal of Theoretical Biology*, 272(1):113–122, March 2011. ISSN 0022-5193. doi: 10.1016/j.jtbi.2010.12.006. WOS:000287227700012.
- Nis S. Jacobsen, Henrik Gislason, and Ken H. Andersen. The consequences of balanced harvesting of fish communities. *Proceedings of the Royal Society B: Biological Sciences*, 281(1775):20132701, January 2014. ISSN 0962-8452, 1471-2954. doi: 10.1098/rspb.2013.2701. URL http://rspb.royalsocietypublishing.org/content/281/1775/20132701.
- Shaun S. Killen, Isabel Costa, Joseph A. Brown, and A. Kurt Gamperl. Little left in the tank: metabolic scaling in marine teleosts and its implications for aerobic scope. *Proceedings of the Royal Society B: Biological Sciences*, 274(1608):431–438, July 2007. ISSN 0962-8452, 1471-2954. doi: 10.1098/rspb.2006.3741. PMID: 17164208.
- R. Law, J. A. Cuesta, and G. W. Delius. Plankton: the paradox and the power law. arXiv, 1705.05327, 2016.
- Richard Law, Michael J. Plank, Alex James, and Julia L. Blanchard. Size-spectra dynamics from stochastic predation and growth of individuals. *Ecology*, 90(3):802–811, February 2009. ISSN 0012-9658. doi: 10.1890/07-1900.1.
- Olivier Maury, Blaise Faugeras, Yunne-Jai Shin, Jean-Christophe Poggiale, Tamara Ben Ari, and Francis Marsac. Modeling environmental effects on the size-structured energy flow through marine ecosystems. part 1: The model. *Progress in Oceanography*, 74(4):479–499, September 2007. ISSN 0079-6611. doi: 10.1016/j.pocean.2007.05.002.
- Johan A. J. Metz and O. Diekmann. *The dynamics of physiologically structured populations*. Springer-Verlag, 1986. ISBN 9780387167862.

- Ransom A. Myers and Noel G. Cadigan. Density-dependent juvenile mortality in marine demersal fish. *Canadian Journal of Fisheries and Aquatic Sciences*, 50(8):1576–1590, August 1993. ISSN 0706-652X, 1205-7533. doi: 10.1139/f93-179.
- Robert Henry Peters. The Ecological Implications of Body Size. Cambridge University Press, March 1986. ISBN 9780521288866.
- John G. Pope, Jake C. Rice, Niels Daan, Simon Jennings, and Henrik Gislason. Modelling an exploited marine fish community with 15 parameters results from a simple size-based model. *Ices Journal of Marine Science*, 63(6):1029–1044, July 2006. ISSN 1054-3139. doi: 10.1016/j.icesjms.2006.04.015. WOS:000239691000007.
- W. E. Ricker. Stock and recruitment. Journal of the Fisheries Research Board of Canada, 11(5): 559–623, May 1954. ISSN 0015-296X. doi: 10.1139/f54-039.
- Marie-Joëlle Rochet, Jeremy S. Collie, Simon Jennings, and Stephen J. Hall. Does selective fishing conserve community biodiversity? predictions from a length-based multispecies model. *Canadian Journal of Fisheries and Aquatic Sciences*, 68(3):469–486, March 2011. ISSN 0706-652X. doi: 10.1139/F10-159. WOS:000287978500008.
- A. G. Rossberg, J. E. Houle, and K. Hyder. Stockrecruitment relations controlled by feeding interactions alone. *Canadian Journal of Fisheries and Aquatic Sciences*, 70:1447–1455, 2013.
- Van M. Savage, James F. Gillooly, James H. Brown, Geoffrey B. West, and Eric L. Charnov. Effects of body size and temperature on population growth. *The American Naturalist*, 163(3):429–441, March 2004. ISSN 0003-0147, 1537-5323. doi: 10.1086/381872.
- R.W. Sheldon, A. Prakash, and W. H. Sutcliffe Jr. The size distribution of particles in the ocean. Limnology and Oceanography, 17:327–340, 1972.
- Erik Ursin. On the prey size preferences of cod and dab. Meddelelser fra Danmarks Fiskeri-og Havundersgelser, 7:8598, 1973.
- G. G. Winberg. Rate of metabolism and food requirements of fishes. Fish. Res. Bd. Can. Trans. Ser., 194:1–202, 1956.
- Lai Zhang, Uffe Høgsbro Thygesen, Kim Knudsen, and K. H. Andersen. Trait diversity promotes stability of community dynamics. *Theoretical Ecology*, 6(1):57–69, February 2013. ISSN 1874-1738, 1874-1746. doi: 10.1007/s12080-012-0160-6.

Table 1: Parameters in the model with dimensions and "default" values. For a detailed explanation of the determination of the values see (Hartvig et al., 2011, App. E).

Resource spectrum				
κ	$5\cdot 10^{-3}$	$g^{\lambda-1}/m^3$	Magnitude of the resource spectrum	
λ	2.05	-	Exponent of resource spectrum $(=2-n+q)$	
r_0	4	g^{1-p}/yr	Constant for regeneration rate of resources	
w_{cut}	0.5	g	Upper weight limit of the resource spectrum	
Individu	al growth			
f_0	0.6	-	Initial feeding level	
α	0.6	-	Assimilation efficiency	
h	40^{\dagger}	g^{1-n}/yr	Constant for max. food intake	
n	0.75	-	Exponent for max. food intake	
k_s	4.8^{\dagger}	g^{1-p}/yr	Constant for std. metabolism and activity	
p	0.75	-	Exponent of standard metabolism*	
β	100	-	Preferred predator-prey mass ratio	
σ	1.3^{\P}	-	Width of size selection function	
γ	Eq. (3.17)	$\mathrm{g}^{-q}m^3/\mathrm{yr}$	Constant for volumetric search rate	
q	0.8^{\S}	-	Exponent for volumetric search rate	
Mortalit	у			
ξ	0.1	-	Fraction of body weight containing reserves	
μ_0	3^{\dagger}	g^{1-n}/yr	Constant for background mortality	
Reproduction and recruitment				
w_0	0.5	mg	Offspring weight	
ϵ	0.1	-	Efficiency of offspring production	
$\phantom{aaaaaaaaaaaaaaaaaaaaaaaaaaaaaaaaaaa$	50^{\ddagger}	-	Factor for maximum recruitment in trait-based model	

^{*}Laboratory experiments on fish indicate that the exponent of standard metabolism should be higher, around p=0.86 (Killen et al., 2007; Winberg, 1956). The practical implication of choosing p>n is that a maximum weight for individuals at which all energy, even if f=1, is used for standard metabolism at $W_+=[(\alpha h)/k_s]^{1/(p-n)}$ (Andersen et al., 2008, Eq. 8). Here a value of p=n is used to make the analysis of the model output easier.

 $^{^\}dagger$ Adjusted to a different value than in (Hartvig et al., 2011) to give growth rates similar to growth rates of species in the North Sea.

[¶]The width of the selection function is chosen to be larger in the trait-based model than in the species-based model (Hartvig et al., 2011) to emulate the diversity in prey-preferences of the species within a trait-class. The practical implication of enlarging σ is that the model is more stable (fewer oscillations) (Datta et al., 2010).

 $^{^{\}ddagger}$ This value should be a little higher but it has been lowered to give a stable output which will facilitate analysis of model output.

[§] If the value of the search exponent is set to n a lot of the formulas involving exponential factors and power-laws of β are simplified significantly as these factor then just becomes 1. Therefore using q = n is preferred for analytical work.

Column name	Description	Default value
	Life history paramet	ters
species	Name of the species	Compulsory (no default)
w_inf	The asymptotic mass of the species	Compulsory (no default)
w_{-} mat	Maturation mass. Used to calculate	Compulsory (no default)
	values for ψ . WHAT IS WMAT IN	
	TERMS OF BIOLOGY? Is it the mass	
	at first maturity?	
beta	Preferred predator prey mass ratio	Compulsory (no default)
sigma	Width of prey size preference	Compulsory (no default)
h	Maximum food intake rate. If this is not	Optional (no default)
11	provided, it is calculated using the k_vb	Optional (no delault)
	column. Therefore, either h or k_vb	
	must be provided.	
lr rrb	_	Ontional (no default)
k_vb	The von Bertalanffy K parameter. Only used to calculate \mathbf{h} if that column is not	Optional (no default)
ma **** ***	provided Volumentaire seems note. If this is not	Ontional (no default)
gamma	Volumetric search rate. If this is not	Optional (no default)
	provided, it is calculated using the h col-	
1	umn and other parameters.	- # 0 2
ks	Standard metabolism coefficient	h * 0.2
z0	Background mortality (constant for all	Optional (no default)
	sizes). If this is not provided then z0 is	
	calculated as $z0pre * w_{\infty}^{z0exp}$. z0pre and	
	z0exp have default values of 0.6 and -	
	1/3 respectively.	
k	Activity coefficient	0.0
alpha	Assimilation efficiency	0.6
erepro	Reproductive efficiency	1
w_\min	The size class that recruits are placed	smallest size class of the species size
	in.	spectrum
	Fishing gear parameters (see Section	8.3 for more details).
sel_func	The name of the selectivity function to	"knife_edge".
	be used.	
gear	The name of the fishing gear that selects	Name of the species
<u> </u>	the species. At the moment a species	•
	can only be selected by one gear.	
catchability	The catchability of the fishing gear.	1
other columns	Other parameters used by the selectiv-	
	ity function. For example, if the de-	
	fault "knife_edge" function is used then	
	the parameters "knife_edge_size" must	
	also be specified as columns (see Sec-	
	tion 8.3).	
	,	on 8.4 for more details)
-411	Stock recruitment parameters (see Section	on o.4 for more details).
other columns	Any arguments that appear in the stock-recruitment function must also	
	stock-recruitment tunction must also	I .
	have a column of values (see Section 8.4)	

Table 2: Columns of the species parameters data.frame

Argument	Description	Default value
min_w	The smallest size of the species commu-	0.001
	nity size spectrum. Note that this a dif-	
	ferent w_min to the one in the species pa-	
	rameter data.frame.	
$\max_{\mathbf{w}}$	The largest size of the species size spec-	The largest w_inf in the species parame-
	trum.	ters data.frame * 1.1
$\mathrm{no}_{-}\mathrm{w}$	The number of size bins in the species size	100
	spectrum.	
$\min_{-w_{-}pp}$	The smallest size of the background size	1e-10
	spectrum.	
nowpp	The number of size bins in the back-	$round(no_w) * 0.3$
	ground size spectrum.	
n	The scaling of intake.	2/3
p	The scaling of standard metabolism.	0.7
q	The search volume exponent.	0.8
$r_{-}pp$	The growth rate of the primary produc-	10
_	tivity (the background spectrum).	
kappa	The carrying capacity of the background	1e11
	spectrum.	
lambda	The exponent of the background spec-	2+q-n
	trum.	
w_pp_cutoff	The cut off size of the background spec-	10
40	trum.	
f0	The feeding level of small individuals	0.6
	feeding mainly on the background re-	
	source. Used to calculate h and gamma if	
	they are not provided in the species pa-	
-0	rameter data.frame.	0.6
z0pre	If z0, the mortality from other sources, is	0.6
	not a column in the species data.frame, it	
= 0.5	is calculated as $z0pre * w_{\infty}^{z0exp}$.	n 1
z0exp	See z0pre	n - 1

Table 3: Other parameters to the MizerParams() constructor

Method	Returns	Description
getSSB()	Two dimensional array (time x	Total Spawning Stock Biomass (SSB)
	species)	of each species through time where
		SSB is calculated as the sum of weight
		of all mature individuals.
getBiomass()	Two dimensional array (time x	Total biomass of each species through
	species)	time.
getN()	Two dimensional array (time x	Total abundance of each species
	species)	through time.
getFeedingLevel()	Three dimensional array (time x	Feeding level of each species by size
	species x size)	through time.
getM2()	Three dimensional array (time x	The predation mortality imposed on
	species x size)	each species by size through time.
getFMort()	Three dimensional array (time x	Total fishing mortality on each species
	species x size)	by size through time.
getFMortGear()	Four dimensional array (time x gear x	Fishing mortality on each species by
	species x size)	each gear at size through time.
getYieldGear()	Three dimensional array (time x gear	Total yield by gear and species
	x species)	through time.
getYield()	Two dimensional array (time x	Total yield of each species across all
	species)	gears through time.

Table 4: Summary methods for ${\it MizerSim}$ objects.

Method	Returns	Degamintion
		Description
getProportionOfLargeFish()	A vector with values at each time	Calculates the proportion of
	step.	large fish through time. The
		threshold value can be specified.
		It is possible to calculation the
		proportion of large fish based on
		either length or weight.
getMeanWeight()	A vector with values at each	The mean weight of the commu-
8	saved time step.	nity through time. This is calcu-
	saved time step.	lated as the total biomass of the
		community divided by the total
		abundance.
mat Maara Mara Waimlat ()	Depends on the manager and	
getMeanMaxWeight()	Depends on the measure argu-	The mean maximum weight of
	ment. If measure = "both"	the community through time.
	then you get a matrix with two	This can be calculated by num-
	columns, one with values by	bers or by biomass. See the help
	numbers, the other with values	file for more details.
	by biomass at each saved time	
	step. If $measure = "numbers"$ or	
	"biomass" you get a vector of the	
	respective values at each saved	
	time step.	
getCommunitySlope()	A data frame with four columns:	Calculates the slope of the
3 · · · · · · · · · · · · · · · · · · ·	time step, slope, intercept and	community abundance spectrum
	R^2 value.	through time by performing a
		linear regression on the logged
		total numerical abundance and
		logged body size.

Table 5: Indicator methods for ${\it MizerSim}$ objects.

Plot	Description			
plotBiomass()	Plots the total biomass of each species through time. A time range to be			
	plotted can be specified. The size range of the community can be specified in			
	the same way as the method getBiomass().			
plotSpectra()	Plots the abundance (biomass or numbers) spectra of each species and the			
	background community. It is possible to specify a minimum size which is			
	useful for truncating the plot.			
plotFeedingLevel()	Plots the feeding level of each species against size.			
plotM2()	Plots the predation mortality of each species against size.			
plotFMort()	Plots the total fishing mortality of each species against size.			
plotYield()	Plots the total yield of each species across all fishing gears against time.			
plotYieldGear()	Plots the total yield of each species by gear against time.			
$\operatorname{plot}()$	Produces 5 plots (plotFeedingLevel(), plotBiomass(), plotM2(),			
	plotFMort() and plotSpectra()) in the same window as a summary.			

Table 6: Plot methods for *MizerSim* objects.