

# Developing the mizerReef package - a collection of vignettes

## 1 Introduction

While only a small proportion of coral reef fish species associate closely with live coral, habitat structure strongly influences biodiversity, community structure, and ecosystem service provision [Graham\_2013]. The primary mechanism by which coral reef structures mediate system dynamics is through the provision of predation refuge [Beukers1998, Almany\_2004]. On coral reefs, refuge use is primarily governed by body size, as the most effective refuges fit prey while excluding predators [Hixon\_1993]. This is reflected in the size-structure of coral reef fish assemblages, which tend to follow the size-structure of refuge holes on a given reef [Nash\_2014]. Size spectrum models capture the ways that communities of individuals grow and change trophic level through ontogeny [Scott\_2014]. Since the protection offered by refuges is size-dependent, size-spectrum models can provide unique insights into how the scale and arrangement of benthic structures can impact community dynamics.

The size-spectrum ecosystem model presented in Chapter 2 serves as a valuable predictive tool for understanding high-level outcomes within coral reef ecosystems, but it is limited in its resolution and fails to capture key dynamics such as reproduction.

\hl{ADD:

- Importance of recruitment, density dependence of reproduction, especially in context of supporting ecosystem services
- Importance of fisher behavior - different gear types, size and species restrictions, area closures
- quick review of the other tools we currently have to look at productivity - Morais method - lack of predictive power
- quick mention of importance of habitat complexity in context of supporting ecosystem services

}

The R package Mizer sets up dynamic, multi-species size-spectrum models of fish communities [mizer]. Dynamics are governed by the same McKendrick von-Foerster system of equations that formed the basis for the model described in Chapter 2, with components added to account for density-dependent recruitment, consumer satiation, and ecosystem carrying capacities. However, Mizer was designed to assess the impacts of fishing on pelagic systems and does not capture key drivers of dynamics in coastal regions such as benthic resources and habitat complexity. To provide more accessible predictive tools for ecosystem managers, I have developed an R extension package that modifies mizer to better reflect tropical reef ecology.

This chapter introduces mizerReef, a R extension package for Mizer that makes it easy to set up a size spectrum model for a tropical coral reef ecosystem. The source code for mizerReef is hosted at <https://github.com/cmbeese/mizerReef>. The package can be used to simulate the size spectrum dynamics in a tropical coral reef community. It is not a ‘community assessment’ tool (i.e. it does not ‘fit’ the model to assess the current state of the community) but simulates the potential consequences of various benthic states and fishing patterns, conditional on the model assumptions and parameter values.

## 2 Methods

### 2.1 Functional Groups

This document details the structure of a typical mizerReef model and includes parameters for an example tropical coral reef ecosystem model set up with mizerReef. The model consists of a collection of fish and invertebrate [functional groups](#) supported by a collection of [resources](#). All predator-prey interactions are mediated by habitat structure, which determines the availability of [refuge](#).

Example parameters were chosen to describe a Caribbean coral reef ecosystem. Numerical values for the parameters associated with each section are provided under the “Parameter values” subsections. Many of the parameters were taken from @Rogers\_2014 and @Beese\_2023 to allow for comparison of results.

#### Parameter values

The model includes 2 functional groups of fish as well as a general group of benthic invertebrates. Estimates of observed abundances for each group were used to select reproduction parameters (discussed later) so that the steady state abundances in the model agree with these observations.

Biomass estimates were based on data collected from relatively un-fished reefs within a marine reserve in Bonaire [Rogers\_2014]. Fish less than 10 cm in length were excluded

from analysis as their abundance is not well captured by visual methods [Ackerman\_2000]. The cutoff weight for observed biomass estimates was calculated using published length-weight relationships. The cutoff size is given in Table 1 along with the observed biomass per square meter in grams.

Table 1: Observed biomasses

	Biomass [g/m <sup>2</sup> ]	Cutoff Size [g]
predators	107.26981	25
herbivores	33.79304	25

## 2.2 Size-spectrum dynamics

The model assumes that, to a first approximation, an individual can be characterized by its weight  $w$  and its functional group number  $i$  only. The aim of the model is to calculate the size spectrum  $N_i(w)$ , which is the *density* of individuals of functional group  $i$  and size  $w$ . The number of individuals in a size range is obtained from the density by integrating over the size range, such that  $\int_w^{w+dw} N_i(w)dw$  is the number of individuals of group  $i$  in the size interval  $[w, w + dw]$ . In other words: the number of individuals in a size range is the area under the number density  $N_i(w)$ .

The time evolution of the number density  $N_i(w)$  is described by the McKendrick-von Foerster equation, which is a transport equation describing the transport of biomass from small to large individuals, with an additional loss term due to fish mortality:

$$\frac{\partial N_i(w)}{\partial t} + \frac{\partial g_i(w)N_i(w)}{\partial w} = -\mu_i(w)N_i(w). \quad (1)$$

The individual growth rate  $g_i(w)$  is described below in the [Growth](#) section and the mortality rate  $\mu_i(w)$  is described in the [Mortality](#) section. These rates depend on the structural complexity of the reef and the density of other fish of other sizes, as well as biomass of plankton, algae and detritus resources, making the size-spectrum dynamics non-linear and non-local in very interesting ways. The resulting effects are too complicated to disentangle by pure thought. This is where simulations with the mizer package come in.

There is no need to understand the mathematical notation used in the McKendrick-von Foerster equation to understand its origin: it just says that the rate at which the number of fish in a size bracket increases is the rate at which fish grow into the size bracket from a smaller size minus the rate at which fish grow out of it to a larger size minus the rate at which the fish in the size bracket die.

For the smallest size class, instead of a rate of growth into the size class there is a rate of reproduction of new individuals into that size class. This reproduction will be described below in the [Reproduction](#) section.

### 2.2.1 Growth

Consumers can only grow by consuming food (i.e. plankton, algae, detritus, or other fish), discounting the losses due to metabolic processes. Predation includes a model for the [predator-prey encounter rate](#) and a model for the rate of [consumption](#). The rate at which predators encounter prey is modified by habitat complexity, which provides predation refuge that prevents certain prey from being encountered. Taking into account the rate of [metabolic losses](#), the resulting energy intake can be partitioned in the model as energy allocated to [reproduction](#) and energy allocated to [somatic growth](#).

#### Predator-prey encounter rate

The rate  $E_i(w)$  at which a predator of group  $i$  and weight  $w$  encounters food (mass per time) is obtained by summing over all prey group and integrating over all prey sizes  $w_p$ , weighted by the selectivity factors described below and (where relevant) adding the encounter rates  $E_{A.i}$  of algae and  $E_{D.i}$  of detritus:

$$E_i(w) = \gamma_i(w) \int \sum_j \theta_{ij} V_{ij}(w_p) N_j(w_p) \phi_i(w, w_p) w_p dw_p + E_{A.i}(w) + E_{D.i}(w). \quad (2)$$

The encounter rates for [algae](#) and [detritus](#) are described in later sections.

The overall prefactor  $\gamma_i(w)$  sets the predation power of the predator. It could be interpreted as a search volume or as an attack rate. By default it is assumed to scale allometrically as  $\gamma_i(w) = \gamma_i w^{3/4}$ . In order for  $E_i(w)$  to have units of grams per year, the prefactor  $\gamma_i$  has to have a unit of  $\text{grams}^{-3/4}$  per year.

The  $\theta_{ij}$  matrix sets the interaction strength between predator group  $i$  prey group  $j$ .

$V_{ij}(w_p)$  sets the vulnerability of prey species  $j$  and weight  $w_p$  to predation by predator species  $i$ . Vulnerability is determined by the presence of [predation refuge](#).

The size selectivity is encoded in the predation kernel  $\phi_i(w, w_p)$ . For most groups we use the lognormal predation kernel given as

$$\phi_i(w, w_p) = \exp \left[ \frac{-(\ln(w/w_p/\beta_i))^2}{2\sigma_i^2} \right] \quad (3)$$

if  $w/w_p$  is larger than 1 and zero otherwise. Here  $\beta_i$  is the preferred predator-prey mass ratio and  $\sigma_i$  determines the width of the kernel.

### Parameter values

The predator/prey interaction matrix has entries equal to either 0 (if the groups can not interact) or 1, see Figure 1.

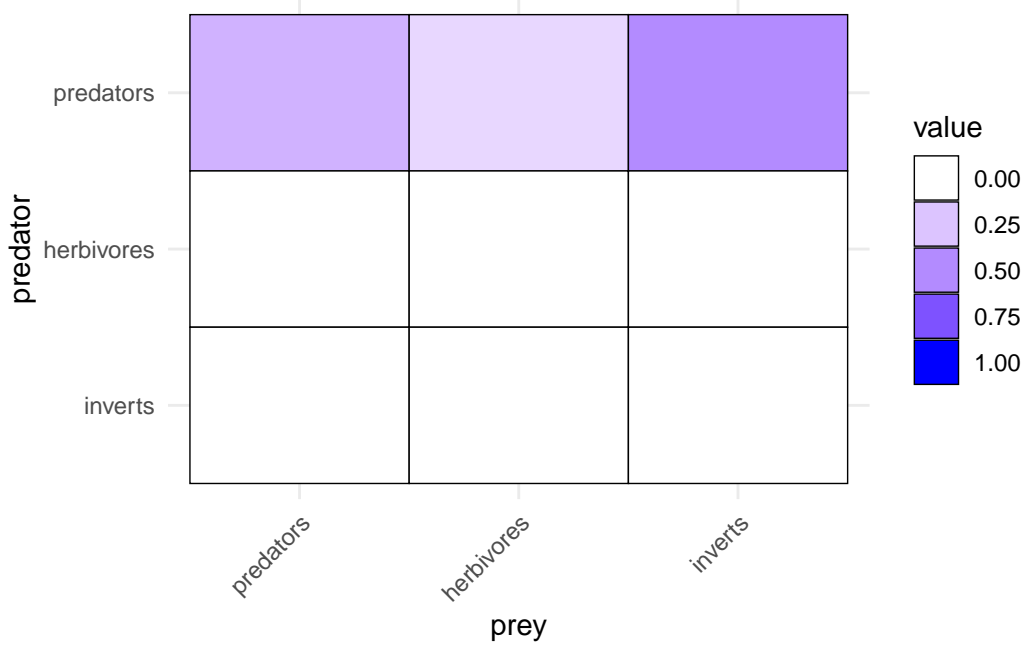


Figure 1: group interaction matrix

The parameters for the predation kernels were chosen to reflect relative differences in foraging preferences between predator functional groups. Initial estimates were based on published PPMR data for several species within each group [REFERENCES FOR PPMR]. These were then adjusted based on functional group characteristics such as preferred prey, predatory mode, and gape size. The parameters are given in Table 2.

Table 2: Parameters for the lognormal predation kernels

	beta	sigma	gamma
predators	100	1	6.4
herbivores	100	1	0.2
inverts	100	1	0.2

### Predation Refuge

Complex biogenic structures mediate the process of predation on reef habitats. To account for this, we reduce the rate at which a predator encounters prey at a level proportional to

the availability of appropriately sized **predation refuges**, which prevent prey fish from being encountered. The refuge function,  $R_j(w_p)$ , describes the proportion of fish of size  $w_p$  in prey group  $j$  that are hidden from predators. We refer to the set of proportions that describe refuge availability across the entire size range of model fish as a **refuge profile**.  $1 - R_j(w_p)$  is then the proportion of fish of weight  $w_p$  and prey group  $j$  that are vulnerable to consumption by predators.

Individuals smaller than  $w_{settle}$  represent pelagic larval fish that have not yet settled to the reef substrate and are too small to utilize refuge to avoid predation. The default value for this minimum weight is 0.1 grams. All individuals below this size are assumed to be vulnerable to predators. To ensure some food is always available, the maximum value of  $R_j(w_p)$  is set to  $R_{max}$ , which defaults to 98%.

Refuge can be suppressed for functional groups which are not expected to utilize biogenic structures for protection (e.g. schooling species) with the [refuge\_user] parameter in the species parameters data frame.

The mizerReef package provides three methods to define the overall refuge profile of a reef depending on the availability of habitat complexity data for the modelled area.

### Sigmoidal

This method is best suited to data-poor reefs or reefs where the refuge distribution is unknown. It is akin to the way refuge was defined in @Rogers\_2014. The proportion of prey of weight  $w_p$  and functional group  $j$  with access to refuge  $R_j(w_p)$  is given by the sigmoid function:

$$R_j(w_p) = \frac{r}{1 + e^{(\alpha(w - W_{refuge}))}} \quad (4)$$

Here  $W_{refuge}$  defines the weight at which refuges transition from being widely available to becoming unavailable.

$r$  defines the maximum proportion of fish with access to predation refuge and is always less than or equal to  $R_{max}$ .

$\alpha$  controls the rate at which the availability of refuge decreases with increasing body size. A smaller  $\alpha$  results in a more gradual decrease in refuge availability, while the default value of 100 results in a steeper decline.

This sigmoid takes on values between 0 and  $R_{max}$ . The body weight at which refuge becomes scarcer for prey is marked by  $W_{refuge}$ .

### Binned

This method is appropriate for theoretical applications and does not rely on complexity data. It is analagous to the way refuge was defined in @Beese\_2023. It sets the availability of refuge to a constant proportion of fish within a given size range. The proportion of fish in functional group  $j$  and weight  $w_p$  with access to refuge  $R_j(w_p)$  is given by:

$$R_j(w_p) = r_k \quad w_p \in (w_{k-1}, w_k] \quad (5)$$

where  $w_p$  is the weight of the prey and  $r_k$  is the proportion of fish with access to refuge in size class  $k$ .

### Competitive

This method is appropriate when **refuge density** data is available for the modeled reef and mirrors the way refuge was defined in @Rogers\_2017 and @Rogers\_2018. The **refuge density** describes the distribution of refuges across defined fish body size categories. The proportion of prey of weight  $w_p$  and functional group  $j$  with access to refuge  $R_j(w_p)$  is given by

$$R_j(w_p) = \min \left\{ R_{max}, \frac{\tau \cdot \eta_k}{\sum_i \int_{w_{k-1}}^{w_k} N_i(w) dw} \quad w_p \in (w_{k-1}, w_k] \right\} \quad (6)$$

The parameter  $\tau$  is the proportion of fish with access to refuge that are expected to utilize it,  $\eta_k$  is the density  $no./m^2$  of refuges in size range  $(w_{k-1}, w_k]$  and  $\sum_i \int_{w_{k-1}}^{w_k} N_i(w) dw$  gives the density  $g/m^2$  of fish from any group in size range  $(w_{k-1}, w_k]$ . This represents the density of competitors for refuges in size class  $k$ .

### Vulnerability

The vulnerability of prey of weight  $w_p$  in group  $j$  to predation by a predator in functional group  $i$  is then given by:

$$V_{ij}(w_p) = 1 - \nu_i \cdot R_j(w_p) \quad (7)$$

where  $\nu_i$  represents whether predators in functional group  $i$  are able to access prey within refuge. For functional groups where  $\nu_i$  is false, some aspect of their morphology or foraging strategy allows them to access prey hidden in refuge; for example large eels that can fit into crevices much smaller than their body size. For these predators, vulnerability for all prey is set to 1.

## Parameter values

The refuge profile gives the proportion of fish at each size that are protected from being encountered by predators, see Figure 2.

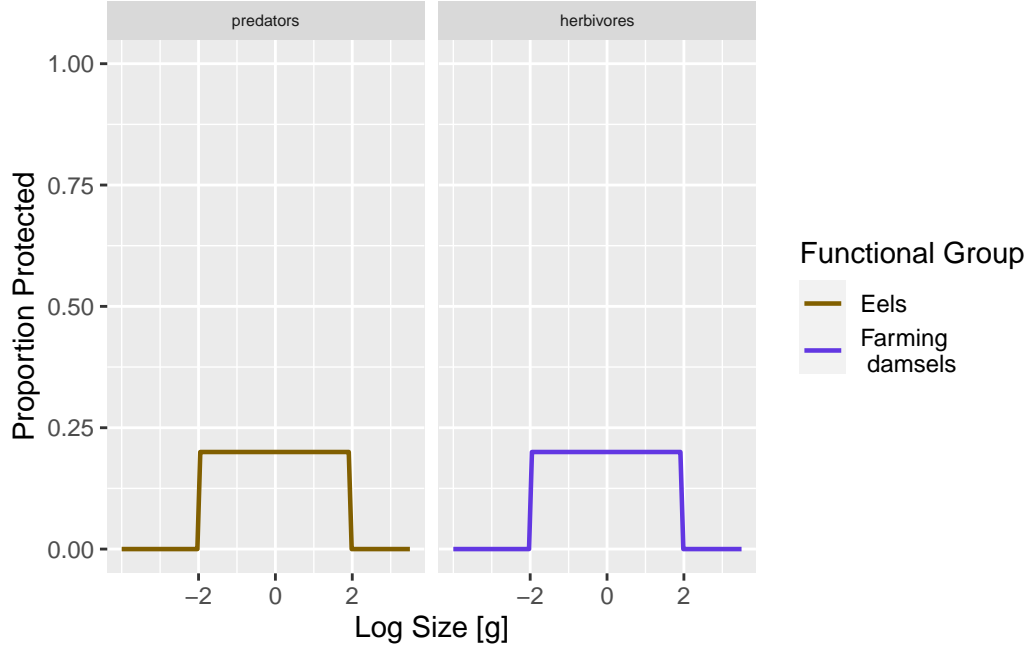


Figure 2: Example refuge profile

Table 3 indicates which prey functional groups use refuge to escape from predators and which predator groups are able to access prey within refuge.

Table 3: refuge behaviour

	Uses refuge?	Accesses prey in refuge?
predators	Yes	No
herbivores	Yes	Yes
inverts	No	Yes

## Consumption

For all non-piscivorous functional groups, encountered food is consumed subject 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.



In mizerReef models, feeding level only applies to herbivorous and detritivorous functional groups. Predation is regulated by refuge, and no maximum intake rate is imposed for piscivores.

The feeding level is given by

$$f_i(w) = \frac{E_i(w)}{E_i(w) + h_i(w)}, \quad (8)$$

where  $h_i(w)$  is the maximum consumption rate of a consumer of group  $i$  and weight  $w$ . By default we assume an allometric form  $h_i(w) = h_i w^n$  with  $n = 0.7$ . The unit of the coefficients  $h_i$  are  $\text{grams}^{1-n}$  per year.

The rate at which food is consumed by an individual of group  $i$  and weight  $w$  is then

$$(1 - f_i(w))E_i(w) = f_i(w) h_i(w). \quad (9)$$

Only a proportion  $\alpha_i$  of this consumed biomass is retained, while a proportion  $1 - \alpha_i$  is expelled in the form of feces, which contribute to detritus.

### Parameter values

No maximum consumption rates were imposed in this example.

Table 4: Consumption parameters

	h	alpha	n
herbivores	Inf	0.6	0.75
inverts	Inf	0.6	0.75

### Metabolic losses

Some of the food consumed is used to fuel the needs for metabolism, activity and movement, at a rate  $\text{metab}_i(w)$ . By default this is made up out of standard metabolism, scaling with exponent  $p$ , and loss due to activity and movement, scaling with exponent 1:

$$\text{metab}_i(w) = k_{s,i} w^p + k_i w. \quad (10)$$

The units of the coefficients  $k_{s,i}$  are  $\text{grams}^{1-p}$  per year and the units of the  $k_i$  is grams per year.

The remaining energy, if any, is then available for growth and reproduction, at the rate

$$E_{r,i}(w) = \max(0, \alpha_i f_i(w) h_i(w) - \text{metab}_i(w)) \quad (11)$$

## Parameter values

Table 5: Metabolism parameters

	ks	p	k
predators	0.10	0.75	0
herbivores	0.15	0.75	0
inverts	0.15	0.75	0

## Investment into reproduction

A proportion  $\psi_i(w)$  of the energy available for growth and reproduction is used for reproduction. This proportion changes from zero below the weight  $w_{mat.i}$  of maturation to one at the maximum weight  $w_{max.i}$ , where all available energy is used for reproduction. The expression is

$$\psi_i(w) = \begin{cases} \left[1 + \left(\frac{w}{w_{mat}}\right)^{-U}\right]^{-1} \left(\frac{w}{w_{max}}\right)^{m-n} & w < w_{max} \\ 1 & w \geq w_{max} \end{cases} \quad (12)$$

with  $m - n = 0.3$  and  $U = 10$  (which sets the steepness of the sigmoidal switch-on of reproduction at around the maturity weight  $w_{mat}$ ).

## Parameter values

Table 6: Parameters determining the investment into reproduction.

	w_mat	w_max
predators	790.5694	3162.278
herbivores	790.5694	3162.278
inverts	790.5694	3162.278

## Somatic growth

What is left over after metabolism and reproduction is taken into account is invested in somatic growth. Thus the growth rate of an individual of functional group  $i$  and weight  $w$  is

$$g_i(w) = E_{r.i}(w) (1 - \psi_i(w)). \quad (13)$$

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

## Parameter values

The values for the model parameters were chosen so that the resulting growth curves would be close to von Bertalanffy growth curves. The parameters in Table 7 were taken from the literature.

Table 7: Parameters for observed vonBertalanffy growth curves and length-weight relationships

	a	b
predators	0.025	3
herbivores	0.025	3
inverts	0.025	3

Here the parameters  $a$  and  $b$  are parameters for the allometric weight-length relationship  $w = al^b$  where  $w$  is measured in grams and  $l$  is measured in centimetres.

### 2.2.2 Mortality

The mortality rate  $\mu_i(w)$  of an individual of group  $i$  and weight  $w$  has three sources: predation mortality  $\mu_{p.i}(w)$ , external mortality  $\mu_{ext.i}(w)$ , fishing mortality  $\mu_{f.i}(w)$ . External mortality is composed of residual natural mortality  $\mu_{nat.i}(w)$ , and senescence  $\mu_{sen.i}(w)$ . The mortality rate for group  $i$  is then given by:

$$\mu_i(w) = \mu_{p.i}(w) + \mu_{ext.i}(w) + \mu_{f.i}(w) \quad (14)$$

We will now explain each of the terms.

#### Predation mortality

All consumption by fish translates into corresponding predation mortalities on the ingested prey individuals. the rate at which all predators from  $j$  consume prey of size  $w_p$  is

$$\text{pred\_rate}_j(w_p) = \int \phi_j(w, w_p)(1 - f_j(w))\gamma_j(w)N_j(w) dw. \quad (15)$$

The mortality rate due to predation is then obtained as

$$\mu_{p.i}(w_p) = \sum_j \text{pred\_rate}_j(w_p) V_{ji}(w_p) \theta_{ji}. \quad (16)$$

### Residual natural mortality

Mortality caused by illness, fishing, or predators not explicitly included in the model is captured by  $\mu_{nat.i}(w)$ , which is independent of the functional groups and group abundances. It is assumed to decrease allometrically with body size:

$$\mu_{nat.i}(w) = \mu_{nat} w^{1-n} \quad (17)$$

where  $\mu_{nat}$  is the residual natural mortality rate and  $n$  is the allometric scaling exponent.

### Parameter values

We use a residual mortality rate of  $\mu_{nat} = 0.2$

### Senescence mortality

Senescence mortality  $\mu_{sen.i}(w)$  is intended to capture mortality due to illness or old age. It is independent of group abundances. Senescence mortality is assumed to increase allometrically with body size. The rate of senescence mortality is given by:

$$\mu_{sen.i}(w) = k_{sen} \left( \frac{\log_{10}(w)}{\log_{10}(w_{max.i})} \right)^{p_{sen}} \quad (18)$$

where  $k_{sen}$  is the rate of senescence mortality,  $p_{sen}$  defines the slope of the senescence curve, and  $w_{max.i}$  is the maximum body size of functional group  $i$  in grams.

### Parameter values

We use a senescence mortality rate of  $k_{sen} = 0.1$  and the exponent  $p_{sen} = 0.3$ .

### Fishing mortality

Like in **mizer**, fishing mortality in **mizerReef** is imposed on functional groups by fishing gears. The total per-capita fishing mortality (1/year) is obtained by summing over the mortality from all gears,

$$\mu_{f.i}(w) = \sum_g F_{g,i}(w),$$

where the fishing mortality  $F_{g,i}(w)$  imposed by gear  $g$  on functional group  $i$  at size  $w$  is calculated as:  $F_{g,i}(w) = S_{g,i}(w)Q_{g,i}E_g$ , where  $S$  is the selectivity by group, gear and size,  $Q$  is the catchability by group and gear and  $E$  is the fishing effort by gear.

Fishing parameters for mizerReef models can be set up with `setFishing()`, which contains the details of how to set up gears with different selectivities and the capabilities of different functional groups.

Fishing mortality  $\mu_{f,i}(w)$  is calculated with the function `getFMort()`.

### Parameter values

Many coral reef fisheries have limited regulation and takes are typically under-reported [Newton\_2007]. For this general example, we use a knife-edge selectivity function which defines a minimum fishing size above which selectivity is 1 for all groups and sizes.

Table 8: Selectivity parameters and catchability

Functional Group	Minimum fishing size [g]	Catchability [1/year]
predators	790.5694	1
herbivores	790.5694	1
inverts	790.5694	1

### Plankton Mortality

The predation mortality rate on the plankton resource  $P$  is given by a similar expression to the predation mortality on fish:

$$\mu_P(w_p) = \sum_j \text{pred\_rate}_j(w_p) \theta_{jP}.$$

### 2.2.3 Reproduction

#### Energy invested into reproduction

The total rate of investment into reproduction (grams/year) is found by integrating the contribution from all individuals of species  $i$ , each of which invests a proportion  $\psi_i(w)$  of their consumption. This total rate of energy investment can then be converted to a rate of production of offspring  $R_{p,i}$  (numbers per year):

$$R_{p,i} = \frac{\epsilon_i}{2w_{min,i}} \int N_i(w) E_{r,i}(w) \psi_i(w) dw. \quad (19)$$

Here the total rate of investment is multiplied by an efficiency factor  $\epsilon$  and then divided by the offspring weight  $w_{min}$  to convert the energy into number of offspring. The result is multiplied by a factor  $1/2$  to take into account that only females contribute directly to offspring.

The size  $w_{min}$  is the egg size.

## Density-dependence in reproduction

Three important density-dependent mechanisms widely assumed in fisheries models are automatically captured in the mizer model, which lead to an emergent stock-recruitment relationship:

1. High density of spawners leads to a reduced food income of the spawners and consequently reduced per-capita reproduction.
2. High density of larvae leads to slower growth of larvae due to food competition, exposing the larvae to high mortality for a longer time, thereby decreasing the survivorship to recruitment size.
3. High density of fish leads to more predation on eggs and fish larvae by other fish species or by cannibalism.

However there are other sources of density dependence that are not explicitly modelled mechanistically in mizer. An example would be a limited carrying capacity of suitable spawning grounds and other spatial effects. This requires additional phenomenological density dependent contributions to the stock-recruitment. In mizer this type of density dependence is modelled through constraints on egg production and survival. The default functional form of this density dependence is represented by a reproduction rate  $R_i$  (numbers per time) that approaches a maximum as the energy invested in reproduction increases. This is described by the common Beverton-Holt type function used in fisheries science:

$$R_i = R_{\max.i} \frac{R_{p.i}}{R_{p.i} + R_{\max.i}}, \quad (20)$$

where  $R_{\max.i}$  is the maximum reproduction rate of species  $i$ .

## Parameter values

The reproduction parameters  $\epsilon_i$  and  $R_{\max.i}$  are not directly observable. The values were instead chosen so as to produce steady-state abundances of the species that are in line with observations and to give reasonable values for the reproduction level.

Table 9 gives the steady-state reproduction level which is defined as the ratio between the actual reproduction rate  $R_i$  and the maximal possible reproduction rate  $R_{\max.i}$ .

Table 9: Parameters determining reproduction

	w_min	erepro	R_max
predators	0.0316228	1	Inf
herbivores	0.0316228	1	Inf
inverts	0.0001000	1	Inf

## 2.3 Resources

The fish spectrum is fed by three background resources: the [plankton spectrum](#), [algae](#), and [detritus](#). Small individuals of all species will feed on plankton while only herbivorous groups and invertebrates feed on algae or detritus. The design of unstructured resources draws from the @mizerShelf model.

### 2.3.1 Plankton Spectrum

The plankton spectrum  $N_P(w)$  tracks the abundance all planktonic food sources. This spectrum starts at a smaller size than the fish spectrum, in order to provide food for the smallest individuals (larvae) of the fish spectrum. The time evolution of the resource spectrum is described by a semi-chemostat equation as in mizer.

The semichemostat dynamics are given by:

$$\frac{\partial N_P(w, t)}{\partial t} = r_P(w) \left[ c_P(w) - N_P(w, t) \right] - \mu_P(w) N_P(w, t).$$

Here  $r_p(w)$  is the plankton regeneration rate and  $c_p(w)$  is the carrying capacity in the absence of predation. By default, mizerReef assumes the same allometric forms as mizer,  $r_P(w) = r_P w^{n-1}$ . and  $c_p(w) = \kappa w^{-\lambda}$ .

The mortality  $\mu_p(w)$  is due to predation by consumers and is described in the subsection [Resource mortality].

#### Parameter values

The plankton spectrum ranges from  $w_0 = 9 \times 10^{-13}$  to  $w_{cutoff} = 1$  grams. The steady state abundance of plankton at size 1g is  $\kappa = 10^{11} [g/m^{-2}]$ . The slope of the plankton spectrum  $\lambda = 2.05$ .

### 2.3.2 Algae

Algae, which consists of macroalgae and turfs, are an important resource for herbivorous reef fish. The algae resource is described only by its total biomass  $B_A$ . Feeding on algae is not is not size-based. Herbivores can feed on algae of any size.

The rate of change in the total algal biomass is simply the difference between the rate at which algal biomass is produced and the rate at which it is consumed, so

$$\frac{dB_A}{dt} = p_A - c_A B_A. \quad (21)$$

We will discuss the production rate  $p_A$  and the consumption rate  $c_A B_A$  below.

### Parameter values

In the steady state the total algal biomass per square meter is  $B_A = 1$  grams.

### Algae consumption

Algae is consumed by herbivorous fish. The rate at which algal biomass is consumed is assumed to be proportional to the available algal biomass. The proportionality factor  $c_A$ , which we refer to as the “mass-specific consumption rate”, depends on the abundance of consumers.

For each consumer species  $i$ , a parameter  $\rho_{A,i}$  determines the rate at which individuals of that species encounter algal biomass. The rate is assumed to scale with the size of the herbivore raised to an allometric exponent  $n$  which is taken to be the same as the scaling exponent of the maximum intake rate for consumers,

$$E_{i,A}(w) = \rho_{i,A} w^n B_A \quad (22)$$

Finally we take into account the preference of herbivorous group  $i$  for algae,  $\theta_{i,A}$ . This gives the mass-specific algal consumption rate:

$$c_A = \sum_i \int \rho_{i,D} w^n N_i(w) \theta_{i,A} dw \quad (23)$$

### Parameter values

The parameters  $\rho_{i,A}$  have units of  $g^{-n}$  per year. They are non-zero only for species that consume at least some algae. The preference  $\theta_{i,A}$  for algae is a value between 0 and 1 specifying the proportion of consumer diets that are comprised of algal matter.

Table 10: Parameters determining rates of algae consumption.

rho	
herbivores	Inf

### Algae production

The rate  $p_A$  at which algae biomass is produced by the ecosystem is given by a constant growth rate with units of grams per unit area per unit time.

### Parameter values

The value of  $p_A$  is 1000 grams per square meter per year.



### 2.3.3 Detritus

Detritus is consumed by herbivores and benthic invertebrates. Feeding on detritus is not size-based as fish can feed on detritus particles of any size. The detritus resource is described only by its total biomass  $B_D$ .

The rate of change in the total detritus biomass is the difference between the rate at which detritus biomass is produced and the rate at which it is consumed, so

$$\frac{dB_D}{dt} = p_D - c_D B_D. \quad (24)$$

The production rate  $p_D$  and the consumption rate  $c_D B_D$  are discussed below.

#### Parameter values

In the steady state the total detritus biomass per square meter is  $B_A = 1$  grams.

#### Detritus consumption

The rate at which detritus biomass is consumed is assumed to be proportional to the available detritus biomass. The proportionality factor  $c_D$ , which we refer to as the “mass-specific consumption rate”, depends on the abundance of consumers.

For each consumer species  $i$ , a parameter  $\rho_{D,i}$  determines the rate at which individuals of that species encounter algal biomass. The rate is assumed to scale with the size of the consumer raised to an allometric exponent  $n$  which is taken to be the same as the scaling exponent of the maximum intake rate for consumers,

$$E_{i,D}(w) = \rho_{i,D} w^n B_D$$

Finally we take into account the preference of species group  $i$  for detritus,  $\theta_{i,D}$ . This gives the mass-specific detritus consumption rate:

$$c_D = \sum_i \int \rho_{i,D} w^n N_i(w) \theta_{i,D} dw$$

## Parameter values

The parameters  $\rho_{i,D}$  have units of  $g^{-n}$  per year. They are non-zero only for species that consume at least some detritus. The preference  $\theta_{i,D}$  for detritus is a value between 0 and 1 specifying the proportion of consumer diets comprised of detritus.

Table 11: Parameters determining rates of algae consumption.

rho	
inverts	Inf

## Detritus production

The rate  $p_D$  at which detritus biomass is produced by the ecosystem has contributions from three sources,

$$p_D = p_{D.f} + p_{D.d} + p_{D.ext}, \quad (25)$$

each of which we will now discuss.

## Feces

$p_{D.f}$  comes from the biomass that is consumed but not assimilated by the predators, i.e., it comes from the feces expelled by the predators. Let  $\alpha_i$  be the proportion of the consumed biomass that is assimilated by species  $i$  and  $E_i(w)$  the food encounter rate discussed in the section on [consumption](#). Then

$$p_{D.f} = \sum_i (1 - \alpha_i) \int E_i(w) dw. \quad (26)$$

## Decomposing Dead Organisms

$p_{D.d}$  comes from the biomass of fish that die as a result of sources of external mortality such as transient predators, illness, and fishing.

This external mortality include senescence and illness deaths that will contribute to detritus, but also deaths due to fishing or predation by species that are not explicitly modelled, for example mammals or sea birds. Thus only a proportion of the external mortality decomposes to detritus. This proportion is given by a detritus parameter `prop_decomp` which defaults to 80% based on the finding that most organic material is recycled in the shallow water systems of coral reefs [Hatcher\_1988]. So

$$p_{D.d} = \sum_i \int \mu_{seni.i}(w) N_i(w) w dw + \text{prop\_decomp} \sum_i \int \mu_{nat.i}(w) N_i(w) w dw.$$

### #### Parameter values

The proportion of mass generated by natural mortality that is converted to detritus is set to the default value of `prop_decomp` = 0.2.

## External

$p_{D.ext}$  is the rate at which detritus enters the system from external sources. This will mostly be detritus sinking in from the pelagic zone. This rate is a model parameter independent of any other model component.

## Parameter values

The value of the external detritus production rate is  $p_{d.ext} = 0.1$  grams per year. This was chosen so that the production and consumption are equal for the chosen steady state abundances.

### 2.3.4 New metrics

Since we may not want to implement fishing mortality directly in mizerReef models, it is valuable to include a tool for estimating how fisheries may respond to changes in the ecosystem. The productivity of a system captures the flow and accumulation of biomass through processes like reproduction, growth, and predation, and does not require estimates of catch. As it cannot be observed directly, it is the perfect candidate for estimation with ecosystem models.

Fisheries productivity refers to the rate at which fish biomass is produced and available for harvest in a given area over a given period of time. This value can be used to estimate the regeneration time of fish stocks and ultimately determine levels of sustainable harvest.

The productivity  $P_i(w)$  of functional group  $i$  is given by

$$P_i(w) = \int_w^{w+dw} N_i(w)g_i(w)dw$$

where  $N_i(w)$  is the abundance density (number per square meter) of functional group  $i$  and  $g_i(w)$  is the energy rate available for growth after metabolism, movement and reproduction have been accounted for in grams per year. To account for gear and size restrictions on fish catches, productivity can be calculated for all fish within a designated size range. As many coral reef fisheries are minimally size and species selective, the default option is to calculate the productivity for all individuals over 7 cm in length regardless of functional group.

## Parameter values

The steady state fisheries productivity for all functional groups is given in Table 12. This simulation reflects a reef with a defined refuge profile with the maximum proportion of refuge  $r = 0.2$  and body size at which refuge becomes scarce  $L_{\text{refuge}} = 15$  cm.

Table 12: Potential fisheries productivity

Productivity [g/m <sup>2</sup> /yr]	
predators	NaN
herbivores	NaN
inverts	NaN

## 3 Vignettes

To demonstrate the use of mizerReef and how dynamics are impacted by parameterisation, we have developed several vignettes that use the described steady state abundances and reproduction parameters.

### 3.1 Changing the minimum size of refuge

In this example we look at the consequences of changing  $L_{\text{refuge}}$ , the body length at which refuge availability rapidly decreases for prey.

#### 3.1.1 Changing the minimum fishing size

Using the simulations from example [the previous section](#), we explore the sensitivity of fisheries productivity to the minimum fishing size parameter.

### 3.2 Simulating fishing mortality

Here we examine how fishing mortality impacts our system. We use knife edge fishing gear.

#### 3.2.1 Restricting fishing on herbivores

Now we can explore how these outcomes might change if fishers only harvested from the predator guild.

### **3.3 Increasing the availability of the algal resource**

There is often a boom in algal resources following mass coral mortality due to bleaching or disturbance, and this can result in an explosion of herbivore populations. Here we investigate model predictions when we increase the availability of the algal resource.

## **4 Conclusion**

The mizerReef package presents a valuable and user-friendly tool with the predictive power to help elucidate outcomes for future reefs in the face of global climate change.