

Model Description

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This document details the structure and parameters for a tropical coral reef ecosystem model. The model consists of a collection of fish and invertebrate [functional groups](#) supported by a collection of [resource spectra](#). All predator-prey interactions are mediated by habitat structure, which determines the availability of [refuge](#). 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 [Beese2023] to allow for comparison of results.

1 Functional Groups

Parameter values

The model includes 9 functional groups of fish as well as a general group of benthic invertebrates. Estimates of observed abundances for each group are not direct model parameters but rather were used to select reproduction parameters (discussed later) so that the steady state abundances in the model agree with these observations.

Biomass estimates for most functional groups were based on data collected in Bonaire [rogers2014]. The survey methods used were unable to detect cryptic or nocturnal species or individuals smaller than 10 cm in length. Biomass estimates for carnivorous eels, nocturnal invertivores, and cryptobenthic predators were taken from the literature [REFERENCE]. The minimum size observed, or cutoff size, for each species is given in Table 1 along with the observed biomass per square meter in grams.

Table 1: Observed biomasses

	Biomass [g/m ²]	cutoff size [g]
eels	0.575	0.0190788
farm_damsel	8.500	0.0204200

	Biomass [g/m ²]	cutoff size [g]
herbs	10.400	0.0323600
inverts	100.000	0.0250000
parrotfish	240.000	0.0257000
pisc_crypt	0.250	0.0922835
pisc_eng	30.000	0.1901017
pisc_grab	200.000	0.0174000
pred_inv	80.000	0.1028903
pred_plank	350.000	0.0125900

1.1 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.

1.2 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](#).

1.2.1 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 γ_i has to have a unit of $\text{grams}^{-3/4}$ per year.

The θ_{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 β_i is the preferred predator-prey mass ratio and σ_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.

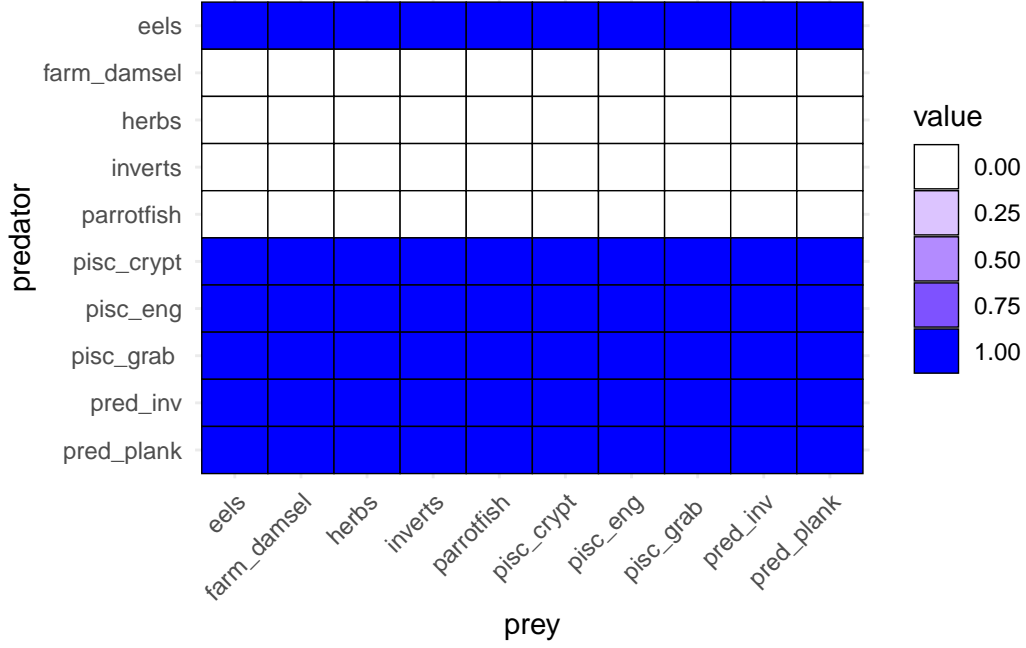


Figure 1: group interaction matrix

The parameters for the predation kernels were estimated based on values found in the literature [REFERENCE]. For the species that use a lognormal predation kernel, the parameters are given in Table 2.

Table 2: Parameters for the lognormal predation kernels

	beta	sigma	gamma
eels	50	2.5	0
farm_damsel	10000	1.0	0
herbs	10000	1.0	0
inverts	100	1.0	0
parrotfish	10000	1.0	0
pisc_crypt	100	2.0	0

	beta	sigma	gamma
pisc_eng	250	2.5	0
pisc_grab	150	1.0	0
pred_inv	5000	2.0	0
pred_plank	8000	1.0	0

1.2.2 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 min group j that are vulnerable to consumption by predators.

Individuals smaller than w_{min} represent pelagic larval fish that have not yet settled to the reef substrate. The default value for this minimum weight is 0.1 grams. All individuals below this size are assumed to be vulnerable to predation. Additionally, 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 complexity data for the modelled area.

Simple Method

This method is best suited to data-poor reefs or reefs where the refuge distribution is unknown. The proportion of prey of weight w_p and functional group j with access to refuge $R_j(w_p)$ is given by:

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

where W_{max} defines the prey body size at which no crevices in the reef are large enough to act as a refuge. Refuge is available to a constant proportion r of fish smaller than W_{max} . The slope α describes the sharpness of the cutoff for fish larger than W_{max} . A shallower slope indicates a more gradual decline in refuge availability with increasing body size. The default value for α sets a steep slope of 100.

Binned Method

This method is appropriate for theoretical applications and does not rely on complexity data. 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 .

Data Method

This method is appropriate when **refuge density** data is available for the modeled reef. 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:

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

where τ is the proportion of fish with access to refuge that are expected to utilize it, η_k is the density 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 total number 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 ν_i represents whether predators in functional group i are able to access prey within refuge. For functional groups where ν_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 encounter by predators, see Figure 2.

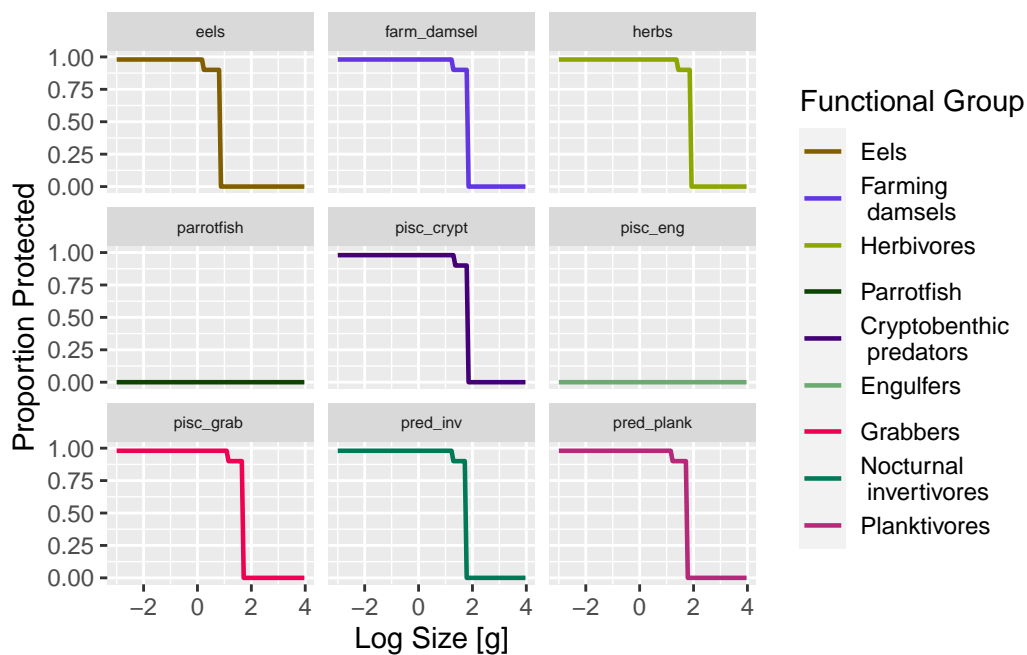


Figure 2: Example refuge profile

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?
eels	Yes	Yes
farm_damsel	Yes	No
herbs	Yes	No
inverts	No	Yes
parrotfish	Yes	No
pisc_crypt	No	Yes
pisc_eng	Yes	No
pisc_grab	Yes	No
pred_inv	Yes	No
pred_plank	Yes	No

1.2.3 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. 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 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 α_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

Feeding level is only applied for non-piscivorous consumers and no maximum consumption rate is imposed for piscivorous functional groups.

For consumers of algae and detritus, the values for the coefficients h_i in the maximum consumption rates were chosen so that the feeding level that fish experience has a reasonable value with fish being neither too starved nor totally satiated.

Table 4: Consumption parameters

	h	alpha
farm_damsel	12.89807	0.6
herbs	93.09740	0.6
inverts	182.19128	0.6
parrotfish	99.88757	0.6

1.2.4 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 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
eels	11.343878	0.75	0
farm_damsel	1.547769	0.75	0
herbs	11.171689	0.75	0
inverts	21.862954	0.75	0
parrotfish	11.986508	0.75	0
pisc_crypt	2.435117	0.75	0
pisc_eng	4.501024	0.75	0
pisc_grab	2.090029	0.75	0
pred_inv	4.715326	0.75	0
pred_plank	5.640335	0.75	0

1.2.5 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
eels	9.5034344	931.845099
farm_damsel	0.5334649	41.540096
herbs	237.7857549	1867.499751
inverts	3.1250000	3125.000000
parrotfish	86.6971203	5035.475034
pisc_crypt	0.3165494	6.242901
pisc_eng	61.1231646	1322.755518
pisc_grab	280.7686892	9307.865716
pred_inv	78.2659574	1600.073891
pred_plank	6.8610153	110.191125

1.2.6 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

	k_vb	a	b
eels	1.0	0.00098	3.24
farm_damsel	0.3	0.02042	2.97
herbs	1.0	0.03236	2.88
inverts	1.0	0.02500	3.00
parrotfish	0.6	0.02570	2.93
pisc_crypt	1.0	0.01122	3.04
pisc_eng	0.4	0.01100	3.11

	k_vb	a	b
pisc_grab	0.1	0.01740	3.01
pred_inv	0.4	0.01200	3.10
pred_plank	1.0	0.01259	3.03

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.

1.3 Mortality

The mortality rate $\mu_i(w)$ of an individual of group i and weight w has two sources: predation mortality $\mu_{p.i}(w)$ and external mortality $\mu_{ext.i}(w)$. 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:

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

We will now explain each of the terms.

1.3.1 Predation mortality

All consumption by fish translates into corresponding predation mortalities on the ingested prey individuals. Recalling that $V_{ij}(w_p)$ is the proportion of prey species i and weight w_p encountered by a predator of group j , the rate at which all predators from j consume prey of size w_p is

$$\text{pred_rate}_j(w_p) = \int \phi_j(w, w_p) \sum_i V_{ij}(w_p) \gamma_j(w) N_j(w) dw. \quad (15)$$

The mortality rate due to predation is then obtained as

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

1.3.2 Residual natural mortality

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

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

where μ_{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 $p_{sen} = 0.3$.

1.4 Reproduction

1.4.1 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 ϵ and then dividing 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 size at which the offspring settle on the reef.

1.4.2 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 ϵ_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 8 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 8: Parameters determining reproduction

	w_min	erepro	R_max
eels	0.001	1	Inf
farm_damsel	0.001	1	Inf
herbs	0.001	1	Inf

	w_min	erepro	R_max
inverts	0.001	1	Inf
parrotfish	0.001	1	Inf
pisc_crypt	0.001	1	Inf
pisc_eng	0.001	1	Inf
pisc_grab	0.001	1	Inf
pred_inv	0.001	1	Inf
pred_plank	0.001	1	Inf

2 Resource Spectra

2.1 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 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.

2.1.1 Parameter values

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

2.1.2 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 9: Parameters determining rates of algae consumption.

	rho
farm_damsel	0.1700618
herbs	0.8592458
parrotfish	0.6585113

2.1.3 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 200 grams per square meter per year.

2.2 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.

2.2.1 Parameter values

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

2.2.2 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 $\rho_{i,D}$ 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 10: Parameters determining rates of algae consumption.

	rho
herbs	0.3682482
inverts	269.8216026
parrotfish	0.6585113

2.2.3 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 α_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`. So

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

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.