

FABM-mizer implementation

Jorn Bruggeman, Bolding & Bruggeman ApS/Plymouth Marine Laboratory

Discretization of the size spectrum

Size-structured models for higher trophic levels are primarily formulated in continuous-size space (Blanchard et al., 2009, 2014; Hartvig et al., 2011). That produces an advection-reaction-type partial differential equation (PDE) that describes the evolution of for total abundance as a function of individual wet mass:

$$\frac{\partial}{\partial t} N(w) = \frac{\partial}{\partial w} (gN) + \dots$$

Here, N denotes abundance (#), w individual wet mass (g), and g individual growth (g time⁻¹). The ... indicates various loss terms associated with predation and natural mortality. In practice the above PDE is usually solved by discretizing individual mass with a first-order upstream scheme, resulting in a model for the evaluation of abundance per size class, N_i . The transfer of mass between two adjacent size bins, characterized by wet masses w_i and w_{i+1} , is given by the instantaneous individual growth rate in bin i (g time⁻¹), divided by the difference in individual wet mass between the bins, $w_{i+1} - w_i$, multiplied by the number of individuals in bin i .

To integrate our implementation of the size-based model with FABM (Bruggeman and Bolding, 2014), and in turn with a wide variety of hydrodynamic models, we compute, but do not time-integrate, the source terms for each size class of fish (as well as prey and waste). These source terms are provided as-is to the hydrodynamic model to be solved (time-integrated) with the same solver it uses for other model variables. Typically, this will be an explicit-in-time solver (cf. Blanchard et al., 2014).

In the section below, we describe the discretised model: equations are given for individual size classes.

Vertical distribution

We assume that the vertical distribution of fish is primarily the result of active swimming by the fish themselves and not the result of water movement. Therefore, biomass in each modelled size class of fish is not modelled as passive tracer subject to hydrodynamic transport (e.g., turbulent mixing). Instead, fish biomass per size class is described by depth-integrated densities (g wet mass m⁻²). As in Cheung et al. (2018), we assume fish distribute instantaneously in the vertical according to their “preference”. Such preference functions can take many forms. Here, we have opted to make the preferred vertical distribution proportional to the total concentration (mg carbon m⁻³) of plankton prey, $P_T(z)$:

$$f(z) = \frac{P_T(z)}{\int P_T(z) dz}$$

This is a probability density with a depth integral of 1 and unit m⁻¹. The same preference distribution is assumed for all size classes of fish. The total concentration of prey itself is the sum of the concentrations of all individual Plankton Functional Types (PFTs) in the lower trophic level model:

$$P_T(z) = \sum_{j=1}^N P_j(z)$$

For instance, that means the sum of 7 PFTs in ERSEM (Butenschön et al., 2016) (table 1).

Table 1. ERSEM plankton functional types and their assigned mass ranges.

ERSEM group	size (wet mass in 10^{-12} g = $1/6 \pi$ ESD in μm)
picoplankton	0.2 – 2 μm ESD
nanophytoplankton	2 – 20 μm ESD
microphytoplankton	20 – 200 μm ESD
diatoms	20 – 200 μm ESD
heterotrophic nanoflagellates	2 – 20 μm ESD
microzooplankton	20 – 200 μm ESD
mesozooplankton	200 μm ESD – 1 mg

As we assume fish distribute rapidly in the vertical, the preference distribution $f(z)$ can be interpreted as measure of the time spent by an individual fish at depth z . For any depth-dependent environmental variable $c(z)$, such as temperature, the effective experienced value is thus $\int f(z)c(z) dz$ (the required normalisation factor $\int f(z)dz$ equals 1 and can therefore be omitted). This formulation implies that if fish are distributed in a very thin layer (e.g., all near the surface), their effective environment is that of that layer only. If fish are distributed homogeneously throughout the water column, the effective environment is the simple average of conditions across the entire column. Similar to the treatment of environmental variables, the vertical distribution of waste production (matter $\text{m}^{-3} \text{time}^{-1}$) is the product of depth-integrated waste production (matter $\text{m}^{-2} \text{time}^{-1}$) and the vertical distribution $f(z)$.

Prey encounter and ingestion

At any depth, the local ingestion in prey biomass time^{-1} for a single predator in size class i is

$$I_i(z) = V_i \sum_{j=1}^{n_p} \phi_{ij} p_j(z)$$

with V_i representing the predator's volumetric search rate ($\text{m}^3 \text{time}^{-1}$), n_p the number of prey types (all plankton functional types and all size classes of fish), $p_j(z)$ the local concentration of the biomass of prey j and ϕ_{ij} the preference of a predator from size class i for prey j . As in Blanchard et al., the preference of a predator with mass w for a prey of mass w_p is a log-normal distribution of the predator : prey mass ratio:

$$\phi(w, w_p) = \exp \left[-\frac{\left(\ln \frac{\beta w_p}{w} \right)^2}{2\sigma^2} \right]$$

This preference function has a maximum of 1 where predator mass is equal to the prey mass multiplied with constant β : the optimal predator-to-prey mass ratio.

For a prey j that is assigned a single mass w_j (e.g., each size class of fish), the above fully specifies the preference of a predator i for such prey:

$$\phi_{ij} = \phi(w_i, w_j)$$

Prey types (PFTs) in the lower trophic level model are assigned a mass range $w_{j,min} - w_{j,max}$ rather than a single mass. To compute the effective preference for such prey, we assume a uniform distribution of prey concentration as function of log prey size within this window;

that is equivalent to a Sheldon (1972) type spectrum for that prey. Under this assumption, the effective preference of predator i for prey j is the average preference over the prey's mass range:

$$\phi_{ij} = \frac{1}{\ln w_{j,max} - \ln w_{j,min}} \int_{\omega=\ln w_{j,min}}^{\ln w_{j,max}} \phi(w_i, e^\omega) d\omega$$

All preferences are independent of prey concentration and can therefore be computed at the start of the simulation from known mass (or mass range) of prey and predator.

The depth-integrated ingestion rate (prey $\text{m}^{-2} \text{time}^{-1}$) per predator in size class i is the integral of local ingestion rates

$$I_{Ti} = \int I_i dz = \int V_i \sum_{j=1}^{n_p} \phi_{ij} p_j(z) f(z) dz = V_i \sum_{j=1}^{n_p} \phi_{ij} \int p_j(z) f(z) dz$$

Here, $\int p_j(z) f(z) dz$ is the depth-averaged concentration of prey j , weighted by the vertical distribution of the predator, $f(z)$. For plankton prey types, the effective prey concentration experienced by the predator is computed directly from $p_j(z)$ and $f(z)$. For prey that are fish from other size classes, the depth-explicit concentration $p_j(z)$ is the product of the depth-integrated density W_j and $f(z)$, which means that the depth-averaged concentration experienced by the predator is

$$\int p_j(z) f(z) dz = W_j \int [f(z)]^2 dz$$

Preference function $f(z)$ appears twice, because it applies both to predator and prey. The resulting factor $\int [f(z)]^2 dz$ has dimension m^{-1} and can be thought of as the reciprocal of an “interaction depth”: the effective depth range over which the fish interact. All predator-prey interactions within the fish community are inversely proportional to this depth.

By substituting prey carbon, nitrogen, phosphorus and silicon (diatoms only) for prey p_j in the above, we obtain separate depth-integrated ingestion rates I_{Ci} for carbon (mmol C time^{-1}), I_{Ni} for nitrogen (mmol N time^{-1}), I_{Pi} for phosphorus (mmol P time^{-1}) and I_{Si} for silicon (mmol Si time^{-1}) per predator. Note that as silicon is not part of fish biomass, its ingestion is tracked only to allow the same quantity to be egested immediately, thus ensuring Si conservation.

Only a fraction α of ingested prey is assimilated. This fraction is assumed to be the same for C, N and P. The unassimilated remainder leaves the fish as through egestion of particulate matter (faeces) or respiration/excretion of dissolved matter. These two fluxes are returned to the lower trophic level model; as they there typically contribute to different pools (dissolved and particulate) they are tracked separately. As in Blanchard et al. (2009) we assume a constant fraction α_{eg} of ingested food is egested. That leaves a fraction $1 - \alpha - \alpha_{eg}$ to be excreted or respired as dissolved matter.

Any maintenance costs for standard metabolism (not active in community mode) are assumed to be energetic costs paid by breaking down carbon (carbohydrates or lipids). Such costs kw (g time^{-1}) are therefore subtracted from the incoming carbon flux only; they do not diminish the availability of nitrogen or phosphorus. The final incoming fluxes of carbon, nitrogen and

phosphorus are converted to the biomass they can produce; the final expression for somatic growth (wet mass in g) per predator is determined by the minimum of the three fluxes

$$g_i = 0.12 \min (\alpha I_{Ci} - kw, \alpha I_{Ni}/q_{NC}, \alpha I_{Pi}/q_{PC})$$

with 0.12 representing the wet mass to carbon ratio (g per mmol) (Boudreau and Dickie, 1992), and $q_{NC} = 16/106$ and $q_{PC} = 1/106$ representing Redfieldian stoichiometric ratios of nitrogen and phosphorus to carbon. These default ratios are based on conventions in marine biogeochemical, modelling. While they fall within the range of ratios observed for fish (Sterner and George, 2000), they could be modified in the future to account for the tendency of higher trophic levels of be richer in phosphorus (Sterner and Elser, 2002). If ingested carbon does not suffice to pay maintenance, a starvation mortality is introduced as in (Blanchard et al., 2014) and somatic growth is set to 0.

Typically, assimilated fluxes of carbon, nitrogen and phosphorus (I_{Ci} , I_{Ni} , I_{Pi}) will not come in the ratio needed for synthesis of fish biomass. With the somatic growth rate g_i set by the most limiting element, excess assimilated fluxes of carbon, nitrogen and phosphorus amount to

$$\begin{aligned} \alpha I_{Ci} - g_i/0.12 \\ \alpha I_{Ni} - q_{NC} g_i/0.12 \\ \alpha I_{Pi} - q_{PC} g_i/0.12 \end{aligned}$$

These excess fluxes are egested and contribute to detritus pools tracked by the lower trophic level model (e.g., the medium size class of detritus, R6, in ERSEM).

Recruitment

As we are describing a community of fish, rather than a single species, there is no straightforward relationship between egg production and the biomass in larger (“adult”) size classes – reproductive effort per size class would depend on species composition, which is unknown. Instead of explicitly modelling reproduction, we therefore let egg production be dictated by the presence of plankton prey. Specifically, we relax the density of the smallest size class of fish (1 mg) towards an expected density that is obtained by extrapolating the depth-integrated plankton size spectrum. The scale factor and exponent of this spectrum are computed at run time by linear regression.

To obtain the plankton size spectrum, we first compute the depth-integrated wet mass of each plankton prey by depth-integrating its carbon concentration (mmol C m⁻³) and multiplying with 0.12 g wet mass per mmol C. We then construct a discretised plankton size spectrum along a log-spaced size axis, spanning $1/\beta^2$ to 1 mg in wet mass with a total of 100 bins. For each bin k , the natural logarithm of wet mass in the centre is denoted by ω_k . The density of each plankton type is assumed to be uniformly distributed (Sheldon et al., 1972) between their predefined size ranges (table 1), which means the final density spectrum (g m⁻²) is a sum of multiple uniform distributions. For each bin k , we then divide the biomass density by the bin width (in g wet mass) to obtain a representation of the spectrum in m⁻² that is independent of its discretisation; finally we then take its natural logarithm, denoted as y_k . We estimate the spectral slope (= exponent on linear scale) through linear regression as

$$a = \frac{\frac{1}{n} \sum \omega_k y_k - \bar{\omega} \bar{y}}{\frac{1}{n} \sum \omega_k^2 - \bar{\omega}^2} \text{ with } \bar{\omega} = \frac{1}{n} \sum \omega_k \text{ and } \bar{y} = \frac{1}{n} \sum y_k$$

The spectral offset (= log of the scale factor on linear scale) is subsequently given by

$$b = \frac{1}{n} \sum y_k - a\omega_k$$

The expected density of the smallest size class of fish (1 mg in wet mass), in g m^{-2} , is then estimated as $\exp[a \ln 0.001 + b]$, multiplied by the bin width of that smallest size class (in g wet mass).

If this expected density of the smallest size class is greater than the current density, the latter is relaxed towards the expected value at a rate of 0.2 d^{-1} . If the expected density is smaller, relaxation is not applied. In this manner, we ensure that effective “recruitment” is always positive.

Natural mortality

Our implementation allows the combination of two types of natural (i.e., non-predation) mortality: a background mortality that is an allometric function of individual mass (or constant, if the allometric exponent is 0) and a senescence mortality that is formulated as allometric function of size starting from a user-selected minimum individual mass (senescence mortality is 0 below that individual mass).

Fishing

As in Scott et al. (2014), our implementation supports several fishing parameterisations, among which “knife edge” (a constant mortality applied to all fish above a user-selected wet mass), logistic selectivity (Blanchard et al., 2014), or a mortality that increases linearly with the logarithm of wet mass (Blanchard et al., 2009). For the community configuration used in this study, we follow Blanchard et al. (2009) in prescribing a fishing mortality (time^{-1}) of

$$F_i = F_A \log_{10} w + F_B$$

for fish larger than 10 g (i.e., $w > 10$).

Biomass removed through application of the fisheries mortality is tracked as “landings” that no longer interact with the ecosystem. Effectively, this reduces the quantities of bioavailable carbon, nitrogen and phosphorus, which if left unchecked would lead to long-term drift of the ecosystem state. Such drift is not known from observations, likely because part of the fished biomass immediately re-enters the system as discards, while loss of the remaining part is compensated by non-local nutrient sources (e.g., riverine inputs). In models that do not explicitly represent riverine sources, such as a one-dimensional GOTM water column (Burchard et al., 2006), we compensate for the loss of biomass due to fisheries by imposing a surface flux of nutrients (nitrate and phosphate) equal to the rate at which those elements are removed through fisheries. No such compensation is needed for carbon, as in most biogeochemical/lower trophic level models the system is open for carbon already: carbon dioxide is exchanged over the water surface.

Temperature dependence

All physiological rates in the model are assumed to be temperature dependent. The default parametrisation is given for an ambient temperature of 13°C . All rates are then scaled with the dimensionless Arrhenius factor:

$$\tau = \exp\left(c_1 - \frac{E_a}{k_B T}\right)$$

With E_a representing activation energy, k_B the Boltzmann constant ($8.62 \times 10^{-5} \text{ eV K}^{-1}$) and T the ambient temperature in Kelvin. Constant c_1 equals $\frac{E_a}{k_B T}$ for reference temperature 286.15 K (13°C). We use $E_a = 0.63$, which implies $c_1 = 25.55$ (Blanchard et al., 2012).

As in Blanchard et al., we apply this temperature dependence to predator-prey interactions (thus growth and predation mortality vary with temperature) and background mortality, but not senescence mortality. Fishing mortality is temperature independent, as it is a prescribed external pressure.

Parameterization

By default, the model is run in Community Size Spectrum Model (CSSM) configuration (Blanchard et al., 2009). Notably, this means prey capture and ingestion is formulated as a linear functional response without saturation or maximum (cf. Blanchard et al., 2014). Metabolic losses (e.g., maintenance) are then implicitly accounted for by using a low efficiency (0.2) for prey-to-biomass conversion, rather than by an explicit standard metabolism loss term (cf. Blanchard et al., 2014). Recruitment is implemented by inferring the density of the lowest size class of fish from the plankton size spectrum, as described above, rather than by linking it to spawning stock biomass.

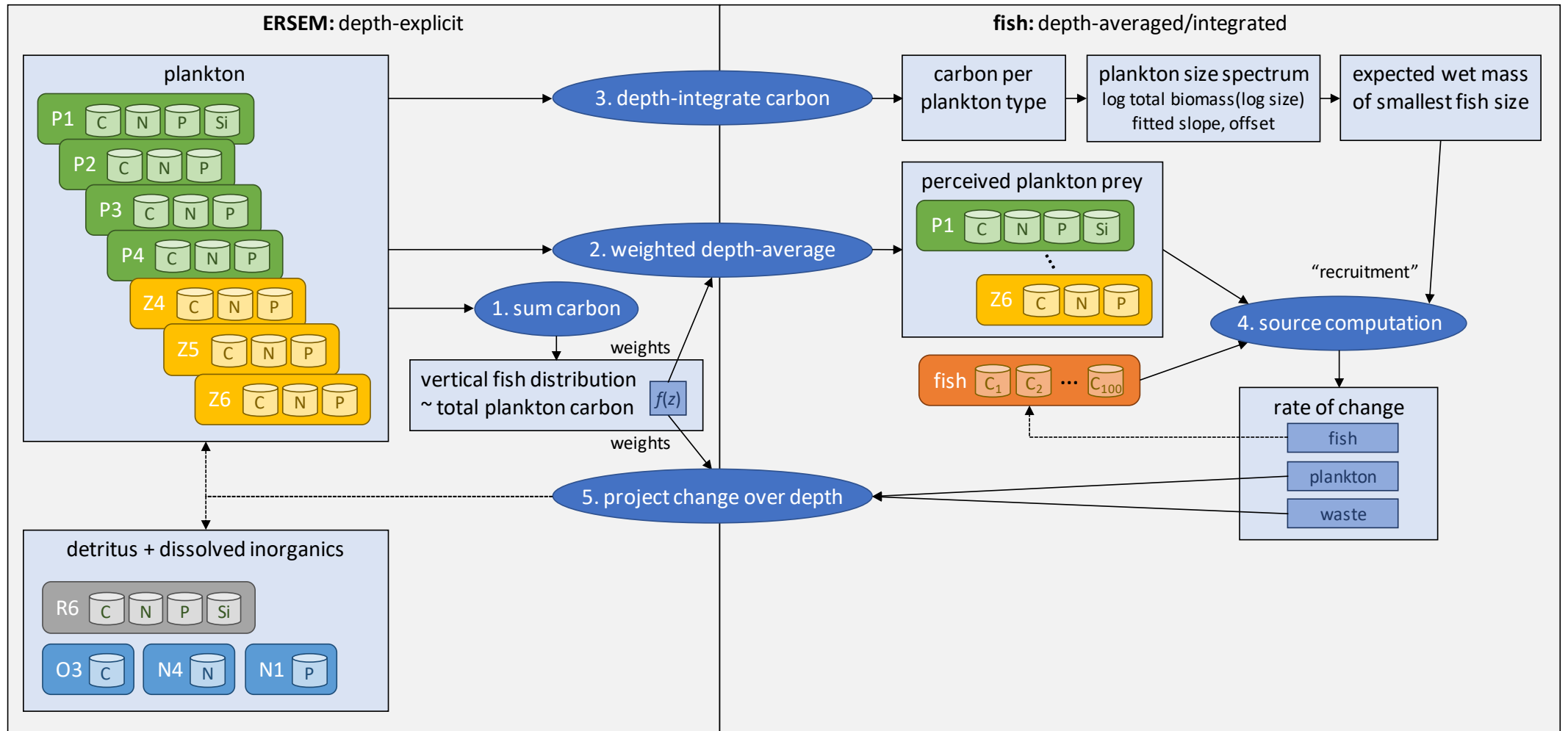


Figure 1. Coupling between a depth-explicit lower trophic level model (ERSEM) and the depth-integrated size-structured fish model. State variables are indicated by cylinder shapes, processes by oval shapes

References

- Blanchard, J. L., Andersen, K. H., Scott, F., Hintzen, N. T., Piet, G., and Jennings, S. (2014). Evaluating targets and trade-offs among fisheries and conservation objectives using a multispecies size spectrum model. *J. Appl. Ecol.* 51, 612–622. doi:10.1111/1365-2664.12238.
- Blanchard, J. L., Jennings, S., Holmes, R., Harle, J., Merino, G., Allen, J. I., et al. (2012). Potential consequences of climate change for primary production and fish production in large marine ecosystems. *Philos. Trans. R. Soc. B-Biological Sci.* 367, 2979–2989. doi:10.1098/rstb.2012.0231.
- Blanchard, J. L., Jennings, S., Law, R., Castle, M. D., McCloghrie, P., Rochet, M.-J., et al. (2009). How does abundance scale with body size in coupled size-structured food webs? *J. Anim. Ecol.* 78, 270–280. doi:10.1111/j.1365-2656.2008.01466.x.
- Boudreau, P. R., and Dickie, L. M. (1992). Biomass Spectra of Aquatic Ecosystems in Relation to Fisheries Yield. *Can. J. Fish. Aquat. Sci.* 49, 1528–1538. doi:10.1139/f92-169.
- Bruggeman, J., and Bolding, K. (2014). A general framework for aquatic biogeochemical models. *Environ. Model. Softw.* 61, 249–265. doi:10.1016/j.envsoft.2014.04.002.
- Burchard, H., Bolding, K., Kühn, W., Meister, A., Neumann, T., and Umlauf, L. (2006). Description of a flexible and extendable physical-biogeochemical model system for the water column. *J. Mar. Syst.* 61, 180–211. doi:10.1016/j.jmarsys.2005.04.011.
- Butenschön, M., Clark, J., Aldridge, J. N., Allen, J. I., Artioli, Y., Blackford, J., et al. (2016). ERSEM 15.06: a generic model for marine biogeochemistry and the ecosystem dynamics of the lower trophic levels. *Geosci. Model Dev.* 9, 1293–1339. doi:10.5194/gmd-9-1293-2016.
- Cheung, W. W. L., Bruggeman, J., and Butenschön, M. (2018). “Projected changes in global and national potential marine fisheries catch under climate change scenarios in the twenty-first century,” in *Impacts of Climate Change on fisheries and aquaculture: Synthesis of current knowledge, adaptation and mitigation options. FAO Fisheries Technical Paper 627*, eds. M. Barange, T. Bahri, M. C. M. Beveridge, K. L. Cochrane, S. Funge-Smith, and F. Poulain (Rome: FAO). Available at: <http://www.fao.org/3/I9705EN/i9705en.pdf>.
- Hartvig, M., Andersen, K. H., and Beyer, J. E. (2011). Food web framework for size-structured populations. *J. Theor. Biol.* 272, 113–122. doi:10.1016/j.jtbi.2010.12.006.
- Scott, F., Blanchard, J. L., and Andersen, K. H. (2014). mizer: an R package for multispecies, trait-based and community size spectrum ecological modelling. *Methods Ecol. Evol.* 5, 1121–1125. doi:10.1111/2041-210X.12256.
- Sheldon, R. W., Prakash, A., and Sutcliffe, W. H. (1972). The size distribution of particles in the ocean. *Limnol. Oceanogr.* 17, 327–340. doi:10.4319/lo.1972.17.3.0327.
- Sterner, R. W., and Elser, J. J. (2002). *Ecological stoichiometry: the biology of elements from molecules to the biosphere*. Princeton, N.J. ; Oxford: Princeton University Press.
- Sterner, R. W., and George, N. B. (2000). Carbon, Nitrogen, and Phosphorus Stoichiometry of Cyprinid Fishes. *Ecology* 81, 127. doi:10.1890/0012-9658(2000)081[0127:CNAPSO]2.0.CO;2.