

SOweb - Model

Andrew Constable

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Contents

A Steady-state Ecosystem Model (SEM)	1
Ecosystem Base	2
Primary production	3
Detritus	4
Nutrients	4
Sources	5
Remineralisation/dissolution	5
Losses	6
Other losses	6
Stoichiometry and micronutrients	6
Spatial variation in sea ice dynamics	6
Consumers in the food web	6
Non-predation mortality & Carcass Pool	7
Estimator	7

A Steady-state Ecosystem Model (SEM)

Generalised production models are well considered in the literature (Yodzis papers from 1992), requiring models of nodes at the base of the food web then driving the food web, in which nodes are constrained by prey as well as other forces.

Creating a steady-state ecosystem model (SEM) allows for a full closure of logic to sustain a food web in perpetuity. Qualitative networks are intended to represent that closure but often only represent a part of the story. Quantitative network models allow for flows between nodes to be expressed but will only demonstrate a balanced representation when the inputs and outputs of the model can be expressed as well. Finding SEMs that arise under specific forcing conditions enables discussions around what forcing factors are important for governing ecosystem structures. They also enable consideration of the pressures and directions of change that one configuration of ecosystem may be under given different or changing forcing conditions.

This process allows simplification of ecosystem structure and function in order to focus on what is known and to minimise the influence of the ‘unknowns’ on the outcomes. Of course, a dynamic system has feedbacks and oscillations which, in reality, are unable to be dampened to a constant state. Understanding inherent variability is not the purpose of this analysis. Instead, it aims to identify whether we can expect gross differences in the underlying relationships given substantial change in the environment. Once (if) identified then the relative importance of variability in driving futures can be focussed on the suite of ‘webs’ that appear possible.

Ecopath with Ecosim relies on estimates of abundance of different biomass pools for scaling a SEM, and for tuning the model i.e. to “estimate” biomasses and trophic linkages that are poorly estimated. It is regarded as a ‘top-down’ ecological model because of its emphasis on balancing food consumption with biomass mortality from predation within a biomass pool. That balance is created by discounting food consumption by metabolic, waste and non-predatory mortality processes. Incorporating ‘bottom up’ processes influencing primary production requires either to scale the biomass of primary producers or by driving the Ecosim component of the system by varying their biomasses through time. The ‘estimation’

process for establishing the starting conditions, i.e. Ecopath, remains unaffected by biogeochemistry and its feedbacks.

The inclusion of nutrient pools and feedbacks to those pools, from recycling of nutrients from trophic excretia, faeces and bodies, is difficult in Ecopath because these pathways are poorly estimated, even though they are well described.

Here, I elaborate a SEM including nutrient feedbacks and switches between different energy pathways based on physiological and ecological limits.

Ecosystem Base

The base of the ecosystem comprises the various nutrient pools, the processes for making these pools available for biological production (bioavailability), and primary production, which transfers energy into the food web. Photosynthesis is the means of energy production in the model presented here but the logic could easily be extended to chemosynthesis.

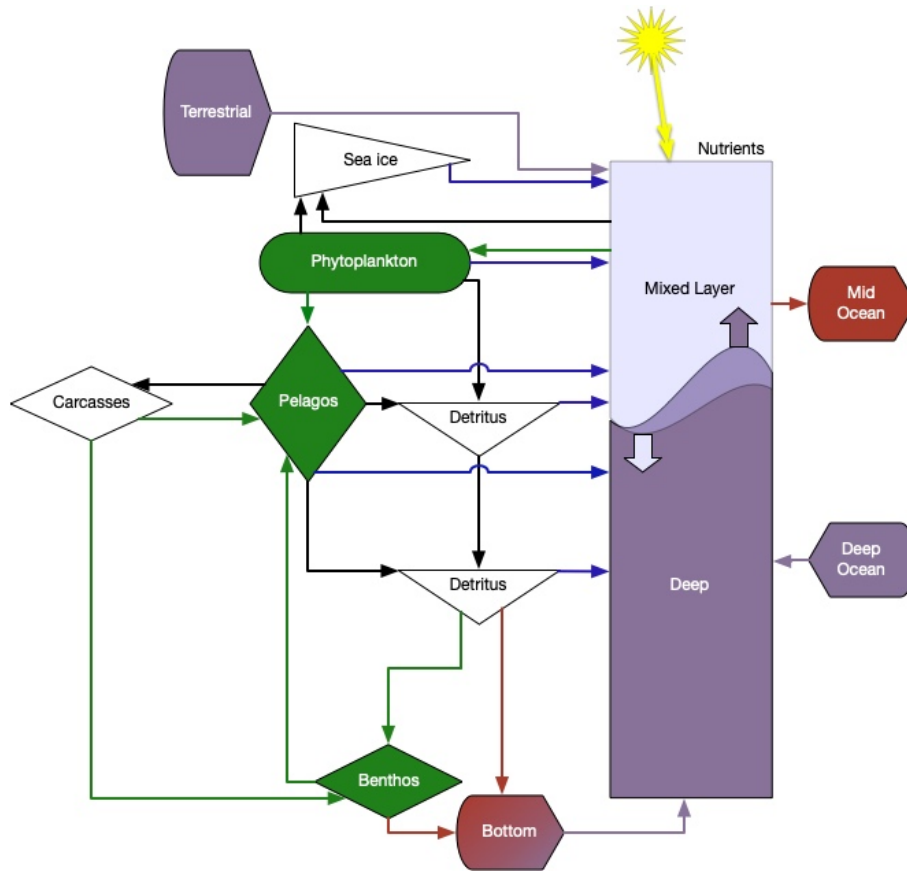


Figure 1: Nutrient flows in the Southern Ocean

The annual advance and retreat of sea ice is difficult to incorporate easily into a steady-state model. This is because the impacts in space and time over a region of interest are not something that can be readily turned into an average cycle of advance and retreat that uniformly affects the region. Some account needs to be given to the proportion of the area that is permanently open ocean, permanently covered by fast ice, and scaled timings of advance and retreat from an area. The equations for nutrient, detrital and primary production pools are developed with a specified seasonal ice dynamic. How these are to be used across a regional steady-state model is considered in a subsequent section.

Biogeochemistry models developed for coupling multiple phytoplankton groups to Earth system models are used as the basis for modelling phytoplankton, detritus and nutrient pools (Hauck et al. 2013; Henson et al. 2021; Fisher et al. 2023; Dutkiewicz et al. 2020).

Primary production

Primary production in the Southern Ocean is primarily governed by temperature in the mixed layer, where primary production occurs, and the available light and nutrients. In the Southern Ocean, the macronutrients, phosphorous and nitrogen, are in abundance. Instead, the region's production is limited by the supply of iron and, in the case of diatoms, silicate (Boyd 2019; Henley 2020). These factors vary in their influence between species (Petrou et al 2016; Boyd 2019) and with latitude and season (Petrou et al 2016; Deppeler & Davidson 2017).

Seasonal variation in mixed layer depth and the presence of sea ice affects the total radiation available to phytoplankton. The proportion (PAR) of surface insolation available for photosynthesis is adopted as a constant. Light is attenuated through water at a constant rate with depth, although the apparent depth of light is greater in winter than summer because of a greater incident angle. Sea ice can also significantly reduces light available to the water column (Perovich 1996); the median ice thickness is approximately 1 m (. For this model, the attenuation through sea ice is regarded as a constant and managed as an additional fraction removed from light (giving a modified PAR*) if sea ice is present, based on attenuation through 1 m of ice.

Inter-specific differences in stoichiometry and cell size mean that production by different species results in differential draw-down rates of the nutrient pools; increased surface to volume ratio of smaller cells increases nutrient uptake rate. Unlike higher trophic levels, primary production and the nutrient pools need to incorporate seasonal changes in these rates, including changes in the mortality rate from consumption, in order to accurately estimate total annual primary production of a taxon. The rate of uptake of nutrients is determined by a Holling Type II and the uptake by the most limiting nutrient (either iron or silicate) determines the rate of growth.

While growth rates of individual taxa are not expected to be independently affected by different factors (Boyd etc), there are no clear multivariate models for growth rates. Hence, classical models for growth rates are adopted here based on the model of Oke et al \citeyear{Oke et al. 2013} but with the effects of light, temperature and nutrient limitation jointly applied (Hauck et al. 2013; Dutkiewicz et al. 2020) and the incident angle of light impacting the attenuation of light with water depth (Melbourne-Thomas et al. 2015).

Thus, growth rates are determined as

$$\begin{aligned}
 J(t, T, \vec{N}, z, SIT) &= \frac{J_{max} \alpha . I(z, t)}{\sqrt{J_{max}^2 + [\alpha . I(z, t)]^2}} . \min(gN_{SiO_3}, gN_{Fe}) \\
 J_{max} &= \mu_{max} * \exp(0.06 * T) \\
 I(z, t) &= I(0, t) . PAR^* . \exp\left(-k_w \frac{z}{\tilde{D}}\right) \\
 \tilde{D} &= \sqrt{1 - \left(\frac{\cos \theta}{1.33}\right)^2} \\
 gN_n &= \frac{c_n N_n}{c_n N_n + \kappa_n}
 \end{aligned} \tag{1}$$

where gN is the functional relationship of phytoplankton, p , consuming nutrient, n . c_p is the degree to which the phytoplankton taxon can compete for the nutrient. This term allows for competition between phytoplankton groups as groups form dense blooms based on the size of the population. Note that this formulation simplifies the relationship between silicate uptake and growth in diatoms, where the growth rate is more rapidly limited with decline silicate (Hauck et al 2013).

While competition amongst phytoplankton groups is not expected in oligotrophic waters (Behrenfeld et al), a competition term, c , is included to allow for when blooms occur and potentially interfere with nutrient access by less dominant species.

Phytoplankton are assumed to be uniformly distributed throughout the mixed layer and spend equal time at all depths. The average growth rate over a 24 hour cycle is used in the steady-state model and determined by integrating growth over the mixed layer and 24 hour day (2τ):

$$\bar{J}(t, MLD) = \frac{2}{MLD} \int_t^\tau \int_z^{MLD} J(I) dz dt \quad (2)$$

With increasing mixed layer depth, cells are expected to redistribute to the additional depth. With a decrease in depth, cells at the bottom depths are lost to the benthic detrital pool or exported from the system. Thus, in units of carbon,

$$\frac{dP_p}{dt} = P_p \left(\bar{J}_p(t, T, \vec{N}) - G_{p \rightarrow z} - \mu_p \right) \mu_p = Sink + Remin + \frac{[\max(\Delta MLD, 0) + \max(\Delta SI, 0)]}{MLD}$$

where \bar{J} is the primary productivity given temperature and the potentially limiting nutrients, G is the grazing by zooplankton, and μ_p is the mortality rate of phytoplankton not associated with grazing, including sinking and remineralisation, and loss through shallowing of the mixed layer or from being trapped in sea ice during freezing. Non-grazing mortality can be a quadratic term but is not applied uniformly in NPZD models. It is not included here but could be easily applied as needed.

Detritus

Detritus is the waste pool of organic fragments originating from dead plankton and the waste from feeding of higher trophic levels, which is either from fragments from eating or faeces (non-assimilated material). This pool is distinguished from carcasses as it can be remineralised as nutrients for primary production or exported. Carcasses, on the other hand, can be preyed on by the food web as carion either in surface waters or in the benthic environment, both of which are described in the food web section below.

Three pools of detritus are included here: the mixed layer pool which contributes to the nutrient pool for primary production, and the deep pool which contributes to benthos and export/sequestration. Importantly the stoichiometry of these pools need to be adjusted according to the stoichiometry of the contributions from different taxa, which is a critical component for this steady state system. For simplicity, three types of pools are distinguished - carbon, iron and silica.

$$dD_m = \sum [(1 - A)(MLD/Range)F_{f \rightarrow s}B_s] - sink(D_m) - remin(dD_m) dD_m^n = \sum [q_f^n(1 - A)(MLD/Range)F_{f \rightarrow s}B_s] - q_f^n$$

$$dD_d = \sum [(1 - A)((Range - MLD)/Range)F_{f \rightarrow s}B_s] + sink(D_m) + sink(P) - remin(dD_d) - Export(dD_d) - Feeding dD_d^n$$

with the equivalent stoichiometries of the Si and Fe components of the detritus being the respective ratios to carbon of each of the components.

text here

Nutrients

A nutrient pool involves the annual availability of nutrients through new and regenerative sources less consumption, export and scavenging. Henley et al (2020) summarise the essential components of the annual nutrient budget. The annual cycle begins with an early winter stoichiometry and abundance in surface waters, which is then added to from various sources, such as upwelling of Circumpolar Deep Water (CDW) and melting of sea ice, coupled with losses to primary production and additions from regeneration of biological waste in the detrital pools. Bioavailability of different micro-nutrients is dependent on chemical and biological processes. While the nutrient model focuses on bioavailable iron because the Southern Ocean is considered to not have limiting nitrates or phosphates, the nutrient model is generalised for any nutrient group.

$$\frac{dN}{dt} = \delta + r - \sum_p s_{pn} \bar{J}_p P_p - L_o \quad (3)$$

comprising the contribution from sources, δ , regeneration/remineralisation from detritus and other biological waste, loss to primary production and other loss through sequestration, export in overturning circulation and other processes such as scavenging of iron. Note that loss to primary production requires a conversion, s , from carbon to the quantity of the relevant nutrient taken up per carbon.

Sources The annual supply of nutrients comes from winter sources for mixing within the surface layer formed in spring coupled with any sources directly inputting to the mixed layer while it is present. The depth of the mixed layer is shallowed by freshwater stratification (ice melt and precipitation) and deepened by winds. In a deterministic system, these sources can be expressed in the following way.

$$\begin{aligned}\delta &= CDW + ICE + be + a \\ CDW &= \bar{N}_{CDW} * \frac{MLD_{W \rightarrow CDW}}{MLD_W} * MLD_S \\ ICE &= \sum_{ice} \bar{N}_{ice} * Melt_{ice} \\ MLD_S &= f(Wind, Melt)\end{aligned}\tag{4}$$

where be and a are constants for benthic sources (geothermal, sediment resuspension) and aeolian inputs respectively, ice types are sea ice and terrestrial ice (glaciers, ice sheet), \bar{N} is the concentration of nutrients per volume water or ice, and $Melt$ is the volume of meltwater from the ice source. Subscripts W and S are for winter and spring respectively. Note that the resetting of nutrients in winter is not simply a replacement of nutrients in surface waters by CDW but a mixing of CDW with the surface waters, thereby diluting the nutrient concentrations from those found in the CDW.

While the role of CDW is likely to be greatest in resetting nutrients by the end of winter, the other sources may have continued contributions throughout the growing season depending on the area in the Southern Ocean and the degree to which they are transported into the mixed layer.

The concentration of nutrients in CDW and Terrestrial Ice sources are considered to be constants, with the latter possibly varied by location around the Antarctic continent for where information is available. The concentration of nutrients in sea ice is dependent on the standing stocks of phytoplankton at the time of sea ice formation, which in turn is influenced by the light and nutrient environments at the timing of freezing. This is considered below as a loss rate for phytoplankton.

Availability of the nutrients for primary production (bioavailability) may need to be factored into this model but, at present, is regarded as a constant for macronutrients.

Remineralisation/dissolution

Remineralisation/dissolution of bioavailable nutrients includes a proportion of the detrital pool becoming available, including remineralisation of dead phytoplankton, and excretion from animals. Thus,

$$r = \mu_d D' + \sum_j \gamma_{2,j} B_j + \sum_p \gamma_{3p} \mu_p P_p$$

where P is primary production, D' is the accumulated detritus during the year and μ are coefficients for the proportion of the pool made bioavailable. ??? is the primary production mortality useful here or should it just go to detritus.???

Remineralisation of iron accompanies remineralisation of carbon from detritus through a dissolved organic state and finally to a bio-available state. This two step process is modelled as a single step by combining the rates of the respective steps. Iron also has a complex chemistry in this dissolved state which is not represented here (Hauck et al 2013). A further complication for iron is scavenging of iron, which is adsorption of iron onto particles, making it unavailable to phytoplankton. This is included in the model.

Losses

Losses of nutrients to primary production are considered further below, noting that the rates will not be constant through the season (Petrou et al 2016, Henley et al 2020).

Stratification (MLD) influencing nutrient availability etc.

timing of sea ice retreat and expansion influences primary production through the shift in the light environment and the timing relative to nutrient depletion. Available phytoplankton in the surface water when freezing occurs will influence nutrient release and seeding when sea ice retreats. . . .

Other losses

Scavenging of iron

Export in overturning circulation

Stoichiometry and micronutrients

what is in the sea ice would otherwise have been lost - it has a longer regeneration time than within year regeneration. . . .

old text

The food web biomass pools can be better constrained by using available nutrient sequestration rates from different pools. One difficulty with other methods for balancing the food web is to pre-specify the dietary composition. This automatically configures the food web to a specific outcome. In order to have greater range for determining what might be an equilibrium position, the trophic relationships need to be more parsimoniously specified, ie. through direct functional feeding relationships as well as conditioning the potential for competition. For example, size-based models do this (S. Jennings and Blanchard 2004; Simon Jennings 2005). In this case per capita feeding rates are determined and used as a basis for consumptive competition (e.g. potential for capture in a single feeding event) and the maximum rate of consumption of each prey type.

Spatial variation in sea ice dynamics

spatial resolution for considering variability in sea ice dynamics scale of areas to be considered is where

how about averaging conditions in latitudinal bands with proportions of different conditions within it - depth strata, etc. this will give shifting light and general seasonal dynamics of sea ice and temperature that fit with the 'rings'. The complex areas of oceanography are generally POOZ and further north.

????The question then is how to translate total consumption of phytoplankton to the appropriate bands in order to get the grazing component correct.????

Consumers in the food web

A modification of the general model of Koen-Alonso & Yodzis (2005) is used here for consumers in the food web in order to explore change in environmental influences on higher trophic levels. While density-dependent mortality may occur, it is not expected to be a great influence when the system is in equilibrium. These influences are not included here but may need to be considered in a dynamic application of these results.

$$\frac{dB_j}{dt} = B_j \left(-T_j + \sum_k e_{kj} F_{kj} \right) - \sum_i B_i F_{ji} - m_j B_j - Y_j$$

explain variables here

There are three important properties of this model that will be influenced by shifts in the environment: 1. **respiration**, which can be affected by temperature in ectotherms and by the foraging effort per biomass consumed 2. **food intake per biomass**, which can be affected by change in the availability of prey generally or by differential changes in availability of parts of the prey population e.g. juveniles 3. **non-predation mortality**, which can result in changing deaths contributing to detrital or carcass pools but not resulting directly from change in predator-prey interactions.

Respiration Yodzis & Quinn (1992) detail the different types of respirers. . .

Food intake Composition of diet is a product of a predator's foraging behaviour, type of prey capture and handling, the availability of prey relative to the predator, and the preferences of the predator given a selection of alternative prey. The dynamics of predators to prey is simplified in dynamic models using some form of functional response (Koen-Alonso & Yodzis, 2005). For the purposes of assessing stable states, a multispecies Type II functional response will be adequate, particularly when it has been found to perform well in modelling the dynamics of marine food webs (Koen-Alonso & Yodzis, 2005). The per biomass consumption of prey, i , by predator, j , is:

$$F_{ij} = \frac{\hat{I}_{ij}\hat{v}_{ij}B_i}{\hat{I}_{ij} + \sum_{i'}\hat{v}_{i'j}B_{i'}}$$

Vulnerability, \hat{v} is included here in place of the term availability as it includes concepts of spatial and depth overlap (availability) combined with selectivity, as in size models, or forms of preference. Vulnerability of prey may change when some prey age classes become more or less exposed to predation. Unpacking \hat{v} gives

$$\hat{v}_{ij}B_i = v(a0)_{ij}w(a0)_i r_i \sum_a mN_a + \sum_a v(a)_{i,j}N_a w_a$$

r is the per adult reproductive success to age zero, $a0$, m is a maturity ogive.

Incorporating age specific vulnerabilities requires solving for age-specific mortality rates if weight at age varies greatly. If adult weight does not vary with age and vulnerability is approximately constant for adults then the equation is easily simplified to solve for changes in either juvenile or adult vulnerabilities and the general vulnerability of the biomass is independent of the age-specific mortality rates, such that:

$$\hat{v}_{ij} = \frac{v_{ij}(a0)w_i(a0) + v_{ij}(a)\bar{w}_i(a)}{(r_iw_i(a0) + \bar{w}_i(a))}$$

Non-predation mortality & Carcass Pool

Describe here the sources of mortality in the food web and how they contribute to the carcass pool which may be preyed on by taxa in the food web.

Estimator

At equilibrium, $\frac{dB_i}{dt}$ equals 0. Thus the ratio $(B + dB/dt)/B = b$ is a measure of the departure of the estimated B from equilibrium because the ratio equals 1 when the vector is at equilibrium. If we assume the ratio is log-normally distributed and the mode, the maximum probability density, is equal to 1 then this ratio can be used in a negative log-likelihood estimator to solve for the vector B . Conceivably, individual B s may range according to the productivity of B . In order to scale the probability density of each biomass to a realistic spread, the standard deviation of the ratio is set as the production to biomass ratio, $\frac{P_i}{B_i}$. As the mode equals 1 then μ equals σ^2 , which is numerically solved from the standard deviation. Thus,

$$Pr(b; \mu, \sigma) = \frac{1}{b\sigma\sqrt{2\pi}} \exp\left(-\frac{(\ln b - \mu)^2}{2\sigma^2}\right) \mu = \sigma^2$$

The negative log-likelihood estimator of the vector \mathbf{B} at equilibrium is

$$L(\vec{B}) = -\sum_i \ln(Pr(b_i; \mu_i, \sigma_i))$$

?? some notes on model fitting General papers for model standardisation and fitting: Hill et al 2021; Pinkerton et al papers. also PREBAL paper by Link 2010

- Dutkiewicz, Stephanie, Pedro Cermeno, Oliver Jahn, Michael J. Follows, Anna E. Hickman, Darcy A. A. Taniguchi, and Ben A. Ward. 2020. "Dimensions of Marine Phytoplankton Diversity." Journal Article. *Biogeosciences* 17 (3): 609–34. <https://doi.org/10.5194/bg-17-609-2020>.
- Fisher, Ben J., Alex J. Poulton, Michael P. Meredith, Kimberlee Baldry, Oscar Schofield, and Sian F. Henley. 2023. "Biogeochemistry of Climate Driven Shifts in Southern Ocean Primary Producers." Journal Article. <https://doi.org/10.5194/bg-2023-10>.
- Hauck, J., C. Volker, T. Wang, M. Hoppema, M. Losch, and D. A. Wolf-Gladrow. 2013. "Seasonally Different Carbon Flux Changes in the Southern Ocean in Response to the Southern Annular Mode." Journal Article. *Global Biogeochem Cycles* 27 (4): 1236–45. <https://doi.org/10.1002/2013GB004600>.
- Henson, S. A., B. B. Cael, S. R. Allen, and S. Dutkiewicz. 2021. "Future Phytoplankton Diversity in a Changing Climate." Journal Article. *Nat Commun* 12 (1): 5372. <https://doi.org/10.1038/s41467-021-25699-w>.
- Jennings, S., and J. L. Blanchard. 2004. "Fish Abundance with No Fishing: Predictions Based on Macroecological Theory." Journal Article. *Journal of Animal Ecology* 73 (4): 632–42. file:///Users%2Fandreworca%2FDesktop%2F_1%2F_pdf%2Fa-z%2FJ%2FJennings_Blanchard_2004.pdf.
- Jennings, Simon. 2005. "Size-Based Analyses of Aquatic Food Webs." Book Section. In *Aquatic Food Webs: An Ecosystem Approach*, edited by Andrea Belgrano, Ursula M. Scharler, Jennifer Dunne, and Robert E. Ulanowicz, 86–97. Oxford: Oxford University Press. file:///Users%2Fandreworca%2FDesktop%2F_1%2F_pdf%2Fa-z%2FJ%2FJennings_2005.pdf.
- Melbourne-Thomas, Jessica, Simon Wotherspoon, Stuart Corney, Ernesto Molina-Balari, Olivier Marini, and Andrew Constable. 2015. "Optimal Control and System Limitation in a Southern Ocean Ecosystem Model." Journal Article. *Deep Sea Research Part II: Topical Studies in Oceanography* 114: 64–73. <https://doi.org/10.1016/j.dsr2.2013.02.017>.
- Oke, P. R., D. A. Griffin, A. Schiller, R. J. Matear, R. Fiedler, J. Mansbridge, A. Lenton, M. Cahill, M. A. Chamberlain, and K. Ridgway. 2013. "Evaluation of a Near-Global Eddy-Resolving Ocean Model." Journal Article. *Geoscientific Model Development* 6 (3): 591–615. <https://doi.org/10.5194/gmd-6-591-2013>.
- Perovich, D. K. 1996. "The Optical Properties of Sea Ice. Monograph 96-1." Report. Cold Regions Research & Engineering Laboratory, US Army Corps of Engineers.