

## SBML Model Report

# Model name: “Elowitz2000 - Repressilator”



May 6, 2016

## 1 General Overview

This is a document in SBML Level 2 Version 3 format. This model was created by the following five authors: Nicolas Le Novre<sup>1</sup>, Bruce Shapiro<sup>2</sup>, Nick Judy<sup>3</sup>, Lukas Endler<sup>4</sup> and Vijayalakshmi Chelliah<sup>5</sup> at January 20<sup>th</sup> 2009 at 2:03 p. m. and last time modified at July tenth 2013 at 10:59 a. m. Table 1 provides an overview of the quantities of all components of this model.

Table 1: Number of components in this model, which are described in the following sections.

Element	Quantity	Element	Quantity
compartment types	0	compartments	1
species types	0	species	6
events	0	constraints	0
reactions	12	function definitions	0
global parameters	16	unit definitions	3
rules	9	initial assignments	0

## Model Notes

### Elowitz2000 - Repressilator

This model describes the deterministic version of the repressilator system.

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The authors of this model (see reference) use three transcriptional repressor systems that are not part of any natural biological clock to build an oscillating network that they called the repressilator. The model system was induced in *Escherichia coli*.

In this system, LacI (variable X is the mRNA, variable PX is the protein) inhibits the tetracycline-resistance transposon tetR (Y, PY describe mRNA and protein). Protein tetR inhibits the gene CI from phage Lambda (Z, PZ: mRNA, protein), and protein CI inhibits lacI expression. With the appropriate parameter values this system oscillates.

This model is described in the article: [A synthetic oscillatory network of transcriptional regulators](#). Elowitz MB, Leibler S. *Nature*. 2000 Jan; 403(6767):335-338

Abstract:

Networks of interacting biomolecules carry out many essential functions in living cells, but the 'design principles' underlying the functioning of such intracellular networks remain poorly understood, despite intensive efforts including quantitative analysis of relatively simple systems. Here we present a complementary approach to this problem: the design and construction of a synthetic network to implement a particular function. We used three transcriptional repressor systems that are not part of any natural biological clock to build an oscillating network, termed the repressilator, in *Escherichia coli*. The network periodically induces the synthesis of green fluorescent protein as a readout of its state in individual cells. The resulting oscillations, with typical periods of hours, are slower than the cell-division cycle, so the state of the oscillator has to be transmitted from generation to generation. This artificial clock displays noisy behaviour, possibly because of stochastic fluctuations of its components. Such 'rational network design' may lead both to the engineering of new cellular behaviours and to an improved understanding of naturally occurring networks.

The model is based upon the equations in Box 1 of the paper; however, these equations as printed are dimensionless, and the correct dimensions have been returned to the equations, and the parameters set to reproduce Figure 1C (left).

The original model was generated by B.E. Shapiro using Cellerator version 1.0 update 2.1127 using Mathematica 4.2 for Mac OS X (June 4, 2002), November 27, 2002 12:15:32, using (PowerMac, PowerPC, Mac OS X, MacOSX, Darwin).

Nicolas Le Novere provided a corrected version generated by SBMLeditor on Sun Aug 20 00:44:05 BST 2006. This removed the EmptySet species. Ran fine on COPASI 4.0 build 18.

Bruce Shapiro revised the model with SBMLeditor on 23 October 2006 20:39 PST. This defines default units and correct reactions. The original Cellerator reactions while being mathematically correct did not accurately reflect the intent of the authors. The original notes were mostly removed because they were mostly incorrect in the revised version. Tested with MathSBML 2.6.0.

Nicolas Le Novere changed the volume to 1 cubic micrometre, to allow for stochastic simulation.

Changed by Lukas Endler to use the average lifetime of mRNA instead of its half-life and a corrected value of  $\alpha$  and  $\alpha_0$ .

Moreover, the equations used in this model were clarified, cf. below.

The equations given in **box 1** of the original publication are rescaled in three respects (lower-case letters denote the rescaled, uppercase letters the unscaled number of molecules per cell):

- the time is rescaled to the average mRNA lifetime,  $\underline{t\_ave} = t/t\_ave$
- the mRNA concentration is rescaled to the translation efficiency  $\underline{eff}$ :  $\underline{m} = M/eff$
- the protein concentration is rescaled to  $\underline{K_M}$ :  $\underline{p} = P/K_M$

in the equations should be in units of rescaled proteins per promotor and cell, and  $\underline{p}$  is the ratio of the protein to the mRNA decay rates or the ratio of the mRNA to the protein halflife.

In this version of the model  $\underline{p}$  and  $\underline{m}$  are calculated correspondingly to the article, while  $\underline{p}$  and  $\underline{m}$  where just replaced by  $\underline{P/K_M}$  resp.  $\underline{M/eff}$  and all equations multiplied by  $\underline{1/t\_ave}$ . Also, to make the equations easier to read, commonly used variables derived from the parameters given in the article by simple rules were introduced.

The parameters given in the article were:

promotor strength (repressed) ( $\underline{tps\_repr}$ ):	(re- $5 \cdot 10^{-4}$ )	transcripts/(promotor*s)
promotor strength (full) ( $\underline{tps\_active}$ ):	0.5	transcripts/(promotor*s)
mRNA half life, $_{1/2,mRNA}$ :	2	min
protein half life, $_{1/2,prot}$ :	10	min
$K_M$ :	40	monomers/cell
Hill coefficient n:	2	

From these the following constants can be derived:

average mRNA lifetime ( $\underline{t\_ave}$ ):	( $\underline{_{1/2,mRNA}} / \ln(2)$ )	= 2.89 min
mRNA decay rate ( $\underline{kd\_mRNA}$ ):	( $\ln(2) / \underline{_{1/2,mRNA}}$ )	= 0.347 min <sup>-1</sup>
protein decay rate ( $\underline{kd\_prot}$ ):	( $\ln(2) / \underline{_{1/2,prot}}$ )	
transcription rate ( $\underline{a\_tr}$ ):	$\underline{tps\_active} * 60$	= 29.97 transcripts/min
transcription rate (repressed) ( $\underline{a0\_tr}$ ):	$\underline{tps\_repr} * 60$	= 0.03 transcripts/min
translation rate ( $\underline{k\_tl}$ ):	$\underline{eff} * \underline{kd\_mRNA}$	= 6.93 proteins/(mRNA*min)
:	$\underline{a\_tr} * \underline{eff} * \underline{_{1/2,prot}} / (\ln(2) * \underline{K_M})$	= 216.4 proteins/(promotor*cell*K <sub>M</sub> )
0 :	$\underline{a0\_tr} * \underline{eff} * \underline{_{1/2,prot}} / (\ln(2) * \underline{K_M})$	= 0.2164 proteins/(promotor*cell*K <sub>M</sub> )
:	$\underline{k\_dp} / \underline{k\_dm}$	= 0.2

Annotation by the Kinetic Simulation Algorithm Ontology (KiSAO):

To reproduce the simulations run published by the authors, the model has to be simulated with any of two different approaches. First, one could use a deterministic method ( [KISAO\\_0000035](#) ) with continuous variables ( [KISAO\\_0000018](#) ). One sample algorithm to use is the CVODE solver ( [KISAO\\_0000019](#) ). Second, one could simulate the system using Gillespie's direct method ( [KISAO\\_0000029](#) ), which is a stochastic method ( [KISAO\\_0000036](#) ) supporting adaptive timesteps ( [KISAO\\_0000041](#) ) and using discrete variables ( [KISAO\\_0000016](#) ).

This model is hosted on [BioModels Database](#) and identified by: [BIOMD0000000012](#) .

To cite BioModels Database, please use: [BioModels Database: An enhanced, curated and annotated resource for published quantitative kinetic models](#) .

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## 2 Unit Definitions

This is an overview of five unit definitions of which two are predefined by SBML and not mentioned in the model.

### 2.1 Unit `volume`

**Name** cubic microns

**Definition** fl

### 2.2 Unit `substance`

**Name** item

**Definition** item

### 2.3 Unit `time`

**Name** minute

**Definition** 60 s

### 2.4 Unit `area`

**Notes** Square metre is the predefined SBML unit for area since SBML Level 2 Version 1.

**Definition** m<sup>2</sup>

### 2.5 Unit `length`

**Notes** Metre is the predefined SBML unit for length since SBML Level 2 Version 1.

**Definition** m

### 3 Compartment

This model contains one compartment.

Table 4: Properties of all compartments.

Id	Name	SBO	Spatial Dimensions	Size	Unit	Constant	Outside
cell		0000290	3	1	litre	<input checked="" type="checkbox"/>	

#### 3.1 Compartment `cell`

This is a three dimensional compartment with a constant size of one fl.

**SBO:0000290** physical compartment

## 4 Species

This model contains six species. Section 8 provides further details and the derived rates of change of each species.

Table 5: Properties of each species.

Id	Name	Compartment	Derived Unit	Constant	Boundary Condition
PX	LacI protein	cell	item	$\square$	$\square$
PY	TetR protein	cell	item	$\square$	$\square$
PZ	cI protein	cell	item	$\square$	$\square$
X	LacI mRNA	cell	item	$\square$	$\square$
Y	TetR mRNA	cell	item	$\square$	$\square$
Z	cI mRNA	cell	item	$\square$	$\square$

## 5 Parameters

This model contains 16 global parameters.

Table 6: Properties of each parameter.

Id	Name	SBO	Value	Unit	Constant
beta	beta		0.200		<input type="checkbox"/>
alpha0	alpha0	0000485	0.216		<input type="checkbox"/>
alpha	alpha	0000186	216.404		<input type="checkbox"/>
eff	translation efficiency	effi-	20.000		<input checked="" type="checkbox"/>
n	n	0000190	2.000		<input checked="" type="checkbox"/>
KM	KM	0000288	40.000		<input checked="" type="checkbox"/>
tau_mRNA	mRNA half life	0000332	2.000		<input checked="" type="checkbox"/>
tau_prot	protein half life	0000332	10.000		<input checked="" type="checkbox"/>
t_ave	average mRNA life time	0000348	0.000		<input type="checkbox"/>
kd_mRNA	kd_mRNA	0000356	0.000		<input type="checkbox"/>
kd_prot	kd_prot	0000356	0.000		<input type="checkbox"/>
k_tl	k_tl	0000016	0.000		<input type="checkbox"/>
a_tr	a_tr	0000186	0.000		<input type="checkbox"/>
ps_a	tps_active	0000186	0.500		<input checked="" type="checkbox"/>
ps_0	tps_repr	0000485	$5 \cdot 10^{-4}$		<input checked="" type="checkbox"/>
a0_tr	a0_tr	0000485	0.000		<input type="checkbox"/>

## 6 Rules

This is an overview of nine rules.

### 6.1 Rule t\_ave

Rule t\_ave is an assignment rule for parameter t\_ave:

$$t_{ave} = \frac{\tau_{mRNA}}{\ln 2} \quad (1)$$

### 6.2 Rule beta

Rule beta is an assignment rule for parameter beta:

$$\beta = \frac{\tau_{mRNA}}{\tau_{prot}} \quad (2)$$

### 6.3 Rule `k_tl`

Rule `k_tl` is an assignment rule for parameter `k_tl`:

$$k\_tl = \frac{eff}{t\_ave} \quad (3)$$

### 6.4 Rule `a_tr`

Rule `a_tr` is an assignment rule for parameter `a_tr`:

$$a\_tr = (ps\_a - ps\_0) \cdot 60 \quad (4)$$

### 6.5 Rule `a0_tr`

Rule `a0_tr` is an assignment rule for parameter `a0_tr`:

$$a0\_tr = ps\_0 \cdot 60 \quad (5)$$

### 6.6 Rule `kd_prot`

Rule `kd_prot` is an assignment rule for parameter `kd_prot`:

$$kd\_prot = \frac{\ln 2}{\tau\_prot} \quad (6)$$

### 6.7 Rule `kd_mRNA`

Rule `kd_mRNA` is an assignment rule for parameter `kd_mRNA`:

$$kd\_mRNA = \frac{\ln 2}{\tau\_mRNA} \quad (7)$$

### 6.8 Rule `alpha`

Rule `alpha` is an assignment rule for parameter `alpha`:

$$\alpha = \frac{a\_tr \cdot eff \cdot \tau\_prot}{\ln 2 \cdot KM} \quad (8)$$

### 6.9 Rule `alpha0`

Rule `alpha0` is an assignment rule for parameter `alpha0`:

$$\alpha0 = \frac{a0\_tr \cdot eff \cdot \tau\_prot}{\ln 2 \cdot KM} \quad (9)$$



## 7 Reactions

This model contains twelve reactions. All reactions are listed in the following table and are subsequently described in detail. If a reaction is affected by a modifier, the identifier of this species is written above the reaction arrow.

Table 7: Overview of all reactions

Nº	Id	Name	Reaction Equation	SBO
1	Reaction1	degradation of LacI transcripts	$X \longrightarrow \emptyset$	0000179
2	Reaction2	degradation of TetR transcripts	$Y \longrightarrow \emptyset$	0000179
3	Reaction3	degradation of CI transcripts	$Z \longrightarrow \emptyset$	0000179
4	Reaction4	translation of LacI	$\emptyset \xrightarrow{X} PX$	0000184
5	Reaction5	translation of TetR	$\emptyset \xrightarrow{Y} PY$	0000184
6	Reaction6	translation of CI	$\emptyset \xrightarrow{Z} PZ$	0000184
7	Reaction7	degradation of LacI	$PX \longrightarrow \emptyset$	0000179
8	Reaction8	degradation of TetR	$PY \longrightarrow \emptyset$	0000179
9	Reaction9	degradation of CI	$PZ \longrightarrow \emptyset$	0000179
10	Reaction10	transcription of LacI	$\emptyset \xrightarrow{PZ} X$	0000183
11	Reaction11	transcription of TetR	$\emptyset \xrightarrow{PX} Y$	0000183
12	Reaction12	transcription of CI	$\emptyset \xrightarrow{PY} Z$	0000183

## 7.1 Reaction `Reaction1`

This is an irreversible reaction of one reactant forming no product.

**Name** degradation of LacI transcripts

**SBO:0000179** degradation

### Reaction equation



### Reactant

Table 8: Properties of each reactant.

Id	Name	SBO
X	LacI mRNA	

### Kinetic Law

**SBO:0000049** mass action rate law for first order irreversible reactions, continuous scheme

**Derived unit** contains undeclared units

$$v_1 = kd.mRNA \cdot X \quad (11)$$

## 7.2 Reaction `Reaction2`

This is an irreversible reaction of one reactant forming no product.

**Name** degradation of TetR transcripts

**SBO:0000179** degradation

### Reaction equation



### Reactant

Table 9: Properties of each reactant.

Id	Name	SBO
Y	TetR mRNA	

### Kinetic Law

**SBO:0000049** mass action rate law for first order irreversible reactions, continuous scheme

**Derived unit** contains undeclared units

$$v_2 = kd\_mRNA \cdot Y \quad (13)$$

### 7.3 Reaction `Reaction3`

This is an irreversible reaction of one reactant forming no product.

**Name** degradation of CI transcripts

**SBO:0000179** degradation

### Reaction equation



### Reactant

Table 10: Properties of each reactant.

Id	Name	SBO
Z	cI mRNA	

### Kinetic Law

**SBO:0000049** mass action rate law for first order irreversible reactions, continuous scheme

**Derived unit** contains undeclared units

$$v_3 = kd\_mRNA \cdot Z \quad (15)$$

### 7.4 Reaction `Reaction4`

This is an irreversible reaction of no reactant forming one product influenced by one modifier.

**Name** translation of LacI

**SBO:0000184** translation

### Reaction equation



## Modifier

Table 11: Properties of each modifier.

Id	Name	SBO
X	LacI mRNA	0000461

## Product

Table 12: Properties of each product.

Id	Name	SBO
PX	LacI protein	

## Kinetic Law

**SBO:0000049** mass action rate law for first order irreversible reactions, continuous scheme

**Derived unit** contains undeclared units

$$v_4 = k_{tl} \cdot X \quad (17)$$

## 7.5 Reaction `Reaction5`

This is an irreversible reaction of no reactant forming one product influenced by one modifier.

**Name** translation of TetR

**SBO:0000184** translation

## Reaction equation



## Modifier

Table 13: Properties of each modifier.

Id	Name	SBO
Y	TetR mRNA	0000461

## Product

Table 14: Properties of each product.

Id	Name	SBO
PY	TetR protein	

### Kinetic Law

**SBO:0000049** mass action rate law for first order irreversible reactions, continuous scheme

**Derived unit** contains undeclared units

$$v_5 = k_{tl} \cdot Y \quad (19)$$

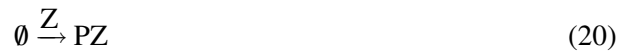
### 7.6 Reaction `Reaction6`

This is an irreversible reaction of no reactant forming one product influenced by one modifier.

**Name** translation of CI

**SBO:0000184** translation

### Reaction equation



### Modifier

Table 15: Properties of each modifier.

Id	Name	SBO
Z	cI mRNA	0000461

### Product

Table 16: Properties of each product.

Id	Name	SBO
PZ	cI protein	

### Kinetic Law

**SBO:0000049** mass action rate law for first order irreversible reactions, continuous scheme

**Derived unit** contains undeclared units

$$v_6 = k_{tl} \cdot Z \quad (21)$$

### 7.7 Reaction [Reaction7](#)

This is an irreversible reaction of one reactant forming no product.

**Name** degradation of LacI

**SBO:0000179** degradation

#### Reaction equation



#### Reactant

Table 17: Properties of each reactant.

Id	Name	SBO
PX	LacI protein	

#### Kinetic Law

**SBO:0000049** mass action rate law for first order irreversible reactions, continuous scheme

**Derived unit** contains undeclared units

$$v_7 = k_{d\_prot} \cdot PX \quad (23)$$

### 7.8 Reaction [Reaction8](#)

This is an irreversible reaction of one reactant forming no product.

**Name** degradation of TetR

**SBO:0000179** degradation

#### Reaction equation



#### Reactant

Table 18: Properties of each reactant.

Id	Name	SBO
PY	TetR protein	

### Kinetic Law

**SBO:0000049** mass action rate law for first order irreversible reactions, continuous scheme

**Derived unit** contains undeclared units

$$v_8 = kd\_prot \cdot PY \quad (25)$$

### 7.9 Reaction [Reaction9](#)

This is an irreversible reaction of one reactant forming no product.

**Name** degradation of CI

**SBO:0000179** degradation

### Reaction equation



### Reactant

Table 19: Properties of each reactant.

Id	Name	SBO
PZ	cI protein	

### Kinetic Law

**SBO:0000049** mass action rate law for first order irreversible reactions, continuous scheme

**Derived unit** contains undeclared units

$$v_9 = kd\_prot \cdot PZ \quad (27)$$

### 7.10 Reaction [Reaction10](#)

This is an irreversible reaction of no reactant forming one product influenced by one modifier.

**Name** transcription of LacI

**SBO:0000183** transcription

### Reaction equation



### Modifier

Table 20: Properties of each modifier.

Id	Name	SBO
PZ	cI protein	0000536

### Product

Table 21: Properties of each product.

Id	Name	SBO
X	LacI mRNA	

### Kinetic Law

**Derived unit** contains undeclared units

$$v_{10} = a_{0\_tr} + \frac{a_{tr} \cdot KM^n}{KM^n + PZ^n} \quad (29)$$

## 7.11 Reaction [Reaction11](#)

This is an irreversible reaction of no reactant forming one product influenced by one modifier.

**Name** transcription of TetR

**SBO:0000183** transcription

### Reaction equation



### Modifier



Table 22: Properties of each modifier.

Id	Name	SBO
PX	LacI protein	0000536

## Product

Table 23: Properties of each product.

Id	Name	SBO
Y	TetR mRNA	

## Kinetic Law

**Derived unit** contains undeclared units

$$v_{11} = a_{0\_tr} + \frac{a_{\_tr} \cdot KM^n}{KM^n + PX^n} \quad (31)$$

### 7.12 Reaction `Reaction12`

This is an irreversible reaction of no reactant forming one product influenced by one modifier.

**Name** transcription of CI

**SBO:0000183** transcription

## Reaction equation



## Modifier

Table 24: Properties of each modifier.

Id	Name	SBO
PY	TetR protein	0000536

## Product

Table 25: Properties of each product.

Id	Name	SBO
Z	cI mRNA	

## Kinetic Law

**Derived unit** contains undeclared units

$$v_{12} = a_{0\_tr} + \frac{a\_tr \cdot KM^n}{KM^n + PY^n} \quad (33)$$

## 8 Derived Rate Equations

When interpreted as an ordinary differential equation framework, this model implies the following set of equations for the rates of change of each species.

Identifiers for kinetic laws highlighted in gray cannot be verified to evaluate to units of SBML substance per time. As a result, some SBML interpreters may not be able to verify the consistency of the units on quantities in the model. Please check if

- parameters without an unit definition are involved or
- volume correction is necessary because the `hasOnlySubstanceUnits` flag may be set to `false` and `spacialDimensions` > 0 for certain species.

### 8.1 Species PX

**Name** LacI protein

**SBO:0000252** polypeptide chain

**Notes** lacI inhibitor

**Initial amount** 0 item

This species takes part in three reactions (as a reactant in [Reaction7](#) and as a product in [Reaction4](#) and as a modifier in [Reaction11](#)).

$$\frac{d}{dt}PX = v_4 - v_7 \quad (34)$$

## 8.2 Species PY

**Name** TetR protein

**SBO:0000252** polypeptide chain

**Notes** Tet repressor protein

**Initial amount** 0 item

This species takes part in three reactions (as a reactant in [Reaction8](#) and as a product in [Reaction5](#) and as a modifier in [Reaction12](#)).

$$\frac{d}{dt}PY = v_5 - v_8 \quad (35)$$

## 8.3 Species PZ

**Name** cI protein

**SBO:0000252** polypeptide chain

**Notes** lambda repressor

**Initial amount** 0 item

This species takes part in three reactions (as a reactant in [Reaction9](#) and as a product in [Reaction6](#) and as a modifier in [Reaction10](#)).

$$\frac{d}{dt}PZ = v_6 - v_9 \quad (36)$$

## 8.4 Species X

**Name** LacI mRNA

**SBO:0000250** ribonucleic acid

**Initial amount** 0 item

This species takes part in three reactions (as a reactant in [Reaction1](#) and as a product in [Reaction10](#) and as a modifier in [Reaction4](#)).

$$\frac{d}{dt}X = v_{10} - v_1 \quad (37)$$

## 8.5 Species Y

**Name** TetR mRNA

**SBO:0000250** ribonucleic acid

**Initial amount** 20 item

This species takes part in three reactions (as a reactant in [Reaction2](#) and as a product in [Reaction11](#) and as a modifier in [Reaction5](#)).

$$\frac{d}{dt}Y = v_{11} - v_2 \quad (38)$$

## 8.6 Species Z

**Name** cI mRNA

**SBO:0000250** ribonucleic acid

**Initial amount** 0 item

This species takes part in three reactions (as a reactant in [Reaction3](#) and as a product in [Reaction12](#) and as a modifier in [Reaction6](#)).

$$\frac{d}{dt}Z = v_{12} - v_3 \quad (39)$$

# A Glossary of Systems Biology Ontology Terms

**SBO:0000016 unimolecular rate constant:** Numerical parameter that quantifies the velocity of a chemical reaction involving only one reactant.

**SBO:0000049 mass action rate law for first order irreversible reactions, continuous scheme:** Reaction scheme where the products are created from the reactants and the change of a product quantity is proportional to the product of reactant activities. The reaction scheme does not include any reverse process that creates the reactants from the products. The change of a product quantity is proportional to the quantity of one reactant. It is to be used in a reaction modelled using a continuous framework.

**SBO:0000179 degradation:** Complete disappearance of a physical entity

**SBO:0000183 transcription:** Process through which a DNA sequence is copied to produce a complementary RNA

**SBO:0000184 translation:** Process in which a polypeptide chain is produced from a messenger RNA

- SBO:0000186 maximal velocity:** Limiting maximal velocity of an enzymatic reaction, reached when the substrate is in large excess and all the enzyme is complexed.
- SBO:0000190 Hill coefficient:** Empirical parameter created by Archibald Vivian Hill to describe the cooperative binding of oxygen on hemoglobine (Hill (1910). The possible effects of the aggregation of the molecules of haemoglobin on its dissociation curves. J Physiol 40: iv-vii)
- SBO:0000250 ribonucleic acid:** Macromolecule formed by a repetition of ribonucleosides linked by phosphodiester bonds. CHEBI:3369
- SBO:0000252 polypeptide chain:** Naturally occurring macromolecule formed by the repetition of amino-acid residues linked by peptidic bonds. A polypeptide chain is synthesized by the ribosome. CHEBI:1654
- SBO:0000288 IC50:** Also called half maximal inhibitory concentration, it represents the concentration of an inhibitor substance that is required to suppress 50% of an effect.
- SBO:0000290 physical compartment:** Specific location of space, that can be bounded or not. A physical compartment can have 1, 2 or 3 dimensions
- SBO:0000332 half-life of an exponential decay:** Time taken by a quantity decreasing according to a mono-exponential decay to be divided by two. Sometimes called  $t_{1/2}$ .
- SBO:0000348 exponential time constant:** Time that it takes for an exponential decay to reach  $1/e$  (about 37%) of the original value. This characterises the frequency response of a first-order, linear time-invariant system. This is also the average lifetime of an element in the decaying set. It is the inverse of the exponential decay constant.
- SBO:0000356 decay constant:** Kinetic constant characterising a mono-exponential decay. It is the inverse of the mean lifetime of the continuant being decayed. Its unit is "per tim".
- SBO:0000461 essential activator:** A substance that is absolutely required for occurrence and stimulation of a reaction
- SBO:0000485 basal rate constant:** The minimal velocity observed under defined conditions, which may or may not include the presence of an effector. For example in an inhibitory system, this would be the residual velocity observed under full inhibition. In non-essential activation, this would be the velocity in the absence of any activator
- SBO:0000536 partial inhibitor:** Substance that, when bound, decreases enzymatic activity to a lower, nonzero value, without itself being consumed or transformed by the reaction, and without sterically hindering the interaction between reactants. The enzyme-inhibitor complex does retain some basal level of activity

SBML<sup>2</sup>AT<sub>E</sub>X was developed by Andreas Dräger<sup>a</sup>, Hannes Planatscher<sup>a</sup>, Dieudonné M Wouamba<sup>a</sup>, Adrian Schröder<sup>a</sup>, Michael Hucka<sup>b</sup>, Lukas Endler<sup>c</sup>, Martin Golebiewski<sup>d</sup> and Andreas Zell<sup>a</sup>. Please see <http://www.ra.cs.uni-tuebingen.de/software/SBML2LaTeX> for more information.

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