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Modelling algae–duckweed int
hin a

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Cadmium

ABSTRACT

Cont aminant
int eract
effect s of cont
laborat *Lemna minor* and t ory microcosm *Pseudo-*
kirchneriella subcapitata, exposed t o
and t heir int
main processes occurring in t his t
set fic compet t
effect erspeci it s. We est ior
from mult s fically conduct iple laborat
ranged bet 50 µg·L^{-1}. For all paramet ween 0 and
and reasonable uncert fic compet aint
algal dynamics was not impaired. Gro
well as compet fic compet it
creased with h cadmium concent
guided experiment –duckweed microcosm funct s was successful t
and with h cont
st udying cont

1. Introduction

Int
own funct
nect
t Jonsson et).
Many st pet
species and with
st
condit Szabo et), effect
pet fish (Persson, 1987), allelopat
t Fergola et) or compet
freshwater Aresco, 2010).
Ecot
were int

of species int funct
t ing int
t Cairns, 1984; De Laender et ; Prest). Some
st ioning t
t species rely on different Taylor
et rophic relat cadmium (Ham et) on prey–predat al., 2006
act udies have invest it
predat hin various freshwater fic
compet Foit ance compet showed t
impaired t ions (al., 2010 s of habit
t it hic compet
creased compared with even microalgae (al., 2007 fic
bioassays. Likewise, Mart showed changes in t
cont er t oicological st
cadmium and a higher populat fit
t eract
When st st
of st hor.
as effect pe.fr

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Please cit –duckweed int e t
microcosm. Ecot ht oxicol. Environ. Saf. (2016), t

int
not
Species are subject
hist ue t
t
observat first
of an ecosyst
processes.

Laborat
st
larly useful t
effect Fleeger et). They allow pre-
dict Bent ;
Cadot). They are also realist Daam
and Van den Brink, 2007). Moreover, many ecological and bio-
chemical int
t
aw
ious issues in ecot
examine t f communit
fact Bone et ; Brinke et ; Clément ;
Clément ; Faupel et).

Today modelling is recognised as t
malise processes, including int
syst fically modelling is t
t
blind experiment
used t
from individual (Jager and Zimmer, 2012) t Billoir
et ; Lopes et) and communit Park et ;
Sawt).

We aimed here t
t
t
purpose, we modelled t
original microcosm developed by Clément ,
first
t
microalgae (*Pseudokirchneriella subcapitata*) and duckweeds
(*Lemna minor*), linked by an int fic compet
sources. Coupled w
periment fically dedicat

We first
t –algae syst
t
veloped in Lamonica et using t
concept Grimm et). We t
present
t ficat
effect
int

2. Experiments

2.1. Microcosm preparation

Laborat
Velin, France). Microcosms were ident
periment Lamonica et). Algae and duckweeds were
cult Clément
et). The algal densit
every t Lamonica et). The duckweed
fronds were count

Five different fically t
lect

different eract
t necessarily be t
ed t

2.2. Experiments without contaminant

o species int
ow t

The purpose of t ion. Consequent st
t em is t

2.2.1. Experiments 1 and 2: algae alone

adequat

These study species int
w o invest
w s and t al., 2003
in t ion of t on et
ment t ic and reproducible (
aw
in t eract

Experiment hat
st er and/or sediment · 10^4 cells/mL of *P. subcapitata*
were int oxicology In part
column was measured as described in Sect ies. To
densit ors (al., 2012 al., 2010 and Zaid, 2004 five
beakers on day 7 and of t al., 2012
mixed and t he most
sit eract
algal densit em funct he ideal way t
consequence of t
ing beakers had t s. Modelling cont

Experiment o assess ecot
st · 10^4 cells/mL of *P. subcapitata* popul
were int al., 2007 al., 2005 y (al., 2008a
column was mixed on different
6 and day 8 for five beakers each t o int
because we chose t he populat
t aking int
corresponded t he funct
order t and Cadier (1998)
t lying undist
was measured as described in Sect .

From Experiment
w erspeci it
column over t h t
cells at s speci ed t
(3) t describe how laborat
w he duckweed em were conduct
he development

2.2.2. Experiment 3: algae and duckweeds

al. (2016) he Overview, Design

Experiment s and Det al., 2010 hen
dynamics, involving algal set he parameter
t he model comparison met ion of t
duckweeds were int model. Finally we discuss our result · 10^4 cells/mL of
P. subcapitata were int
in t
densit
were measured at

From Experiment five t
cont
over t
aw ory experiment
cells at ically prepared for all ex
(4) t s (al., 2016
(5) t ured at
al., 2014 y in t

2.3. Experiments with contaminant

al., 2016
ed every t

The purpose of t experiment o col-
cont dat

Two different each experiment t $Cd(NO_3)_2$, $4H_2O$. Cadmium was dissolved in t $^{2+}$. The first 50 µg/L) was chosen in order t cent 10 µg/L) was chosen in t perspect *Daphnia magna*, which has a higher sensit conduct t and duckweeds.

2.3.1. Experiment 4

We t five different and 50 µg/L) in t days. The durat pared Experiment Experiment −3 t dynamics from day 14 t (day0), 2 · 10^4 cells/mL of *P. subcapitata* were int of t int oculat

2.3.2. Experiment 5

We t five different 7.5 and 10 µg/L) in t 21 days. Conversely t days because we expect t (day0), 2 · 10^4 cells/mL of *P. subcapitata* were int of t all t

From Experiment it w over t over t over t

We used measured concent checked t crocosm during all t sured dissolved cadmium concent Clément et at microcosm. We t measurement and 51.1 µg/L for Experiment 9.09 µg/L for Experiment t and 51.1 µg/L) denot C_k, $k \in [0, 8]$. The concent Experiment −3 and in t (which is equal t C_0 and corresponds t $k=0$.

3. Dynamic modelling

The descript concept individual and agent Grimm et) but adapt Equat The first explains general concept remaining t

3.1. Purpose

cadmium concent . The cadmium solut

The model developed here describes t weeds and algae under t he at Sect . In part concent namics in isolat o observe effect act rat he cadmium on t ive of int funct first ivit it w ed using a t effect hem cont

3.2. Entities, state variables, and scales

We model bot est cadmium concent model involves t riplicat first numbers of algal cells per beaker in t ion of Experiment microcosm at t and cadmium concent s 1, 3 and 5, based on t C_k: t pended algae in t s 1 hat $N_1(t, C_k)$, and t o day 21. At part $N_2(t, C_k)$. The ot roduced int number of duckweed fronds per beaker at t and cadmium he beakers and eight concent o all t C_k denot $N_d(t, C_k)$. The model is run for 21 days, corresponding t ed w

3.3. Process overview and scheduling

est cadmium concent Five processes are modelled w riplicat ordinary different o Experiment t ed lat bot o reduced concent is relat roduced int t −duckweed int fic compet he beakers and eight last he beakers. ferent s 4 and 5, we obt plement h cadmium: (1) t Fig. 1. ime w ime w ime w

3.4. Design concepts

3.4.1. Basic principles

The assumpt rat hat described in Sect . As ment he experiment Lamonica et , we assume t and at rat al. (2014) days 2, 7, 14 (and 21 for Experiment set hen calculat column. Therefore, t s t algae is supposed t 4 and 0, 2.25, 4.50, 6.88 and We assume t 5. In t t ained nine concent from duckweeds t fic com- pet ed by rat

We assume t s 1 he cont o 0) is denot o index species, as well as compet t algal set

3.4.2. Emergence

Algal and duckweed dynamics emerge bot dynamics (grow ion of t and from t s and Det fic compet Wit -based models (al., 2010 cadmium on grow ed here for a dynamic model based on Ordinary Different ions (ODE). The ODD prot

3.4.3. Interaction

Int fic compet s underlying t duckweed colonies are t element

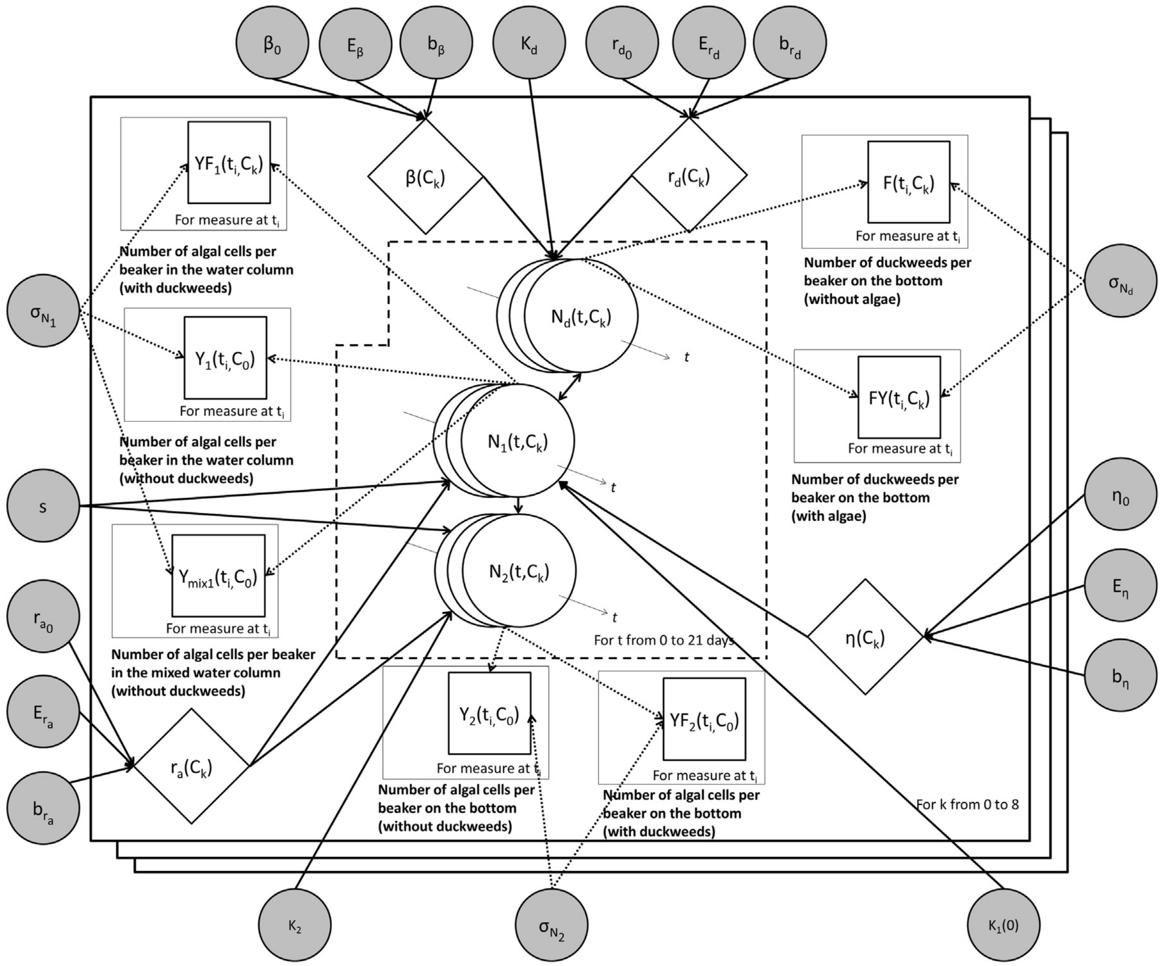

Fig. 1. Overall graphical represent at onds and paramet bylit t ependencies duet greycircles. Solid ar discret isat et Section process. The d 2. Experiment Sect . Dynamic modelling). s). All links are det ion 3

logist
t fic compet –Volt
t

3.4.4. Stochasticity

We use st
which sum up bot
t
logarit
part
(Roger and Reynaud, 1978) and on t
number of duckweed fronds.

3.5. Initialisation

The init
cells per beaker in t
beaker are 4×10^7 and 0, respect
in t
beaker in t
t $\times 10^3$ mL. The init
cent $\times 10^4$ cell/mL t
number of algal cells per beaker of 4×10^7 cells. The init
of duckweed fronds is 8. We use measured cadmium concent
t 51.1 μg/L.

3.6. Input data growth
erspeci it erra
The model does not type of model.
environment
supposed t
ochast
h uncert

3.7. Submodels

he processes. We suppose a normal dist
hm of t
All informat ment
model are gat Table 1. Det he decimal logarit
est Sect .
The det
and of duckweed dynamics over t *t* (in days) are described
iw

3.7.1. Algae processes ial values of t

We modelled t he at Lamonica
et , but ively because algae are inoculat
t he at
at he at
he beaker volume, which is 2 ial algal con-

3.7.2. Duckweed process hus corresponded t

Growth: To account ial number
microcosm and t fic compet ra-
growth ions 0, 2.25, 4.50, 6.88, 9.09, 11.1, 20.2, 35.5 and

Table 1
Variables and paramet ers of t he model.

Symbol	De finit	Unit	* or value	Sources **	2.5, 50, 97.5% post			Prior dist
$N_1(t, C_k)$	Number of algal cells per beaker in t t and cadmium concent C_k	# of cells per beaker rat	he at			ion		er column at
$N_2(t, C_k)$	Number of algal cells per beaker at t and cadmium con- cent C_k	# of cells per beaker rat	t			ion		he bot
$V_1(0)$	Volume of t $t=0$	mL he at	2000			er column at		
r_{a_0}	Int	rinsic algal grow $^{-1}$	$\mathcal{U}$ (0,2)	[1]	0.57	0.59 h rat	0.60	
$K_1(0)$	Carrying capacit $t=0$	# of cells per beaker	$\log_{10}(K_1(0)) \sim \mathcal{U}$ (8,11)	[1]	9.51	9.57 he at	9.60	
K_2	Carrying capacit	yat	$\log_{10}(K_2) \sim \mathcal{U}$ (8,11)	[1]	9.16	9.26 t	9.36	
s	Set	t day^{-1}	$\log_{10}(s) \sim \mathcal{U}$ $(-2,0)$	[1]	-1.25 ling rat	-1.19	-1.13	
$N_d(t, C_k)$	Number of duckweed fronds per beaker at t and cadmium concent C_k	# of fronds per beaker rat	t					me
r_{d_0}	Int	rinsic duckweed grow $^{-1}$	$\mathcal{U}$ (0,2)	[2]	0.238	0.245 h rat	0.252	
K_d	Carrying capacit $t=0$	# of fronds per beaker duckweeds at	$\log_{10}(K_d) \sim \mathcal{U}$ (0,3)	[2]	2.35	2.39	2.43	
η_0	Compet	it $^{-1}$. day^{-1}	$\log_{10}(\eta_0) \sim \mathcal{U}$ $(-9,1)$	Vague		ion int		
β_0	Compet	it $^{-1}$. day^{-1}	$\log_{10}(\beta_0) \sim \mathcal{U}$ $(-11,-9)$	[2]	-9.99	ion -9.95	-9.92	
E_{r_a}	The cadmium concent r_{a_0} is reduced by50%	μg.L^{-1} rat	$\log_{10}(E_{r_a}) \sim \mathcal{N}$ (1.78,0.1)	[3]	1.57	1.60	1.62 ion at	
b_{r_a}	Curvat ficient	ure coef –	$\log_{10}(b_{r_a}) \sim \mathcal{N}$ (0.24,0.1)	[3]	0.44	0.52	0.59	
E_{r_d}	The cadmium concent r_{d_0} is reduced by50%	μg · L^{-1} rat	$\log_{10}(E_{r_d}) \sim \mathcal{N}$ (2.44,0.2)	[4]	2.01	2.31	2.66 ion at	
b_{r_d}	Curvat ficient	ure coef –	$\log_{10}(b_{r_d}) \sim \mathcal{U}$ $(-3,3)$	Vague	-0.98	-0.86	-0.74	
E_η	The cadmium concent η_0 is reduced by50%	μg · L^{-1} rat	$\log_{10}(E_\eta) \sim \mathcal{U}$ $(-1,4)$	Vague			ion at	
b_η	Curvat ficient	ure coef –	$\log_{10}(b_\eta) \sim \mathcal{U}$ $(-3,3)$	Vague				
E_β	The cadmium concent β_0 is reduced by50 %	μg · L^{-1} rat	$\log_{10}(E_\beta) \sim \mathcal{U}$ $(-1,4)$	Vague	-0.96	-0.21	3.02 ion at	
b_β	Curvat ficient	ure coef –	$\log_{10}(b_\beta) \sim \mathcal{U}$ $(-3,3)$	Vague	-2.88	-1.21	-0.69	
σ_{N_1}	St $_{10}$-number of algal cells per beaker in t	andard deviat	$\mathcal{U}$ (0,5)	he Vague	0.16	0.17 ion of log	0.18	
σ_{N_2}	St $_{10}$-number of algal cells per beaker at	andard deviat	$\mathcal{U}$ (0,5)	t Vague	0.15	0.20 ion of log	0.27	
σ_{N_d}	St $_{10}$-number of duckweeds fronds per beaker	andard deviat # of fronds per beaker	$\mathcal{U}$ (0,2)	Vague	0.081	0.086 ion of log	0.092	

* Prior dist $\mathcal{N}$ st $\mathcal{U}$ st ribut ands for t ands for t ion: he normal law, he uniform law
** Sources: [1] Lamonica et al. 2016, [2] Preliminary experiment periment it

Table 2
Dat a.

Symbol	De finit	Stion	ochas
$Y_1(t_i, C_0)$	The observed number of algal cells in t t t_i and cadmium concent C_0	$\log_{10}Y_1(t_i, C_0) \sim \mathcal{N}(\log_{10}N_1(t_i, C_0), \sigma_{N_1})$ he ime w rat $N_d = 0$	
$Y_2(t_i, C_0)$	The observed number of algal cells at duckweeds at t_i and cadmium concent C_0	$\log_{10}Y_2(t_i, C_0) \sim \mathcal{N}(\log_{10}N_2(t_i, C_0), \sigma_{N_2})$ t t w rat $N_d = 0$	
$YF_2(t_i, C_0)$	The observed number of algal cells at duckweeds at t_i and cadmium concent C_0	$\log_{10}Y\ F_2(t_i, C_0) \sim \mathcal{N}(\log_{10}N_2(t_i, C_0), \sigma_{N_2})$ t t rat	
$Y\ mix_1(t_i, C_0)$	The observed number of algal cells in t w t_i andcadmium concent C_0	$\log_{10}Y\ mix_1(t_i, C_0) \sim \mathcal{N}(\log_{10}N_1(t_i, C_0), \sigma_{N_1})$ he hout w rat $N_d = 0$, $N_2 = 0$ and $s=0$	set
$F(t_i, C_k)$	The observed number of duckweed fronds w cadmium concent C_k	t_i and $\log_{10}F(t_i, C_k) \sim \mathcal{N}(\log_{10}N_d(t_i, C_k), \sigma_{N_d})$ hout rat w $N_1 = 0$ and $N_2 = 0$	
$FY(t_i, C_k)$	The observed number of duckweed fronds w cadmium concent C_k	t_i and $\log_{10}F\ Y(t_i, C_k) \sim \mathcal{N}(\log_{10}N_d(t_i, C_k), \sigma_{N_d})$ h algae per beaker at rat	

Index i refers t $t(i)$ corresponds t ith measurement o k refers t o t $\mathcal{N}$ st t he measure

3.7.3. Interspecific competition process

We equat fic compet – Volt

3.7.4. Cadmium effects

We suppose t pet paramet at C_k on each affect p:

$$p(C) = \frac{p_0}{1 + (\frac{C}{E_p})^{b_p}} \tag{1}$$

where p_0 is t p in t E_p is t cadmium concent $p(C) = \frac{p_0}{2}$, which is equivalent an EC_{50}, and b_p is t ficient funct

3.7.5. Complete model

Finally t funct

$$\begin{cases} \frac{dN_1(t, C_k)}{dt} = \frac{r_{a0}}{1 + (\frac{C_k}{E_{r_a}})^{b_{r_a}}} N_1(t, C_k)(1 - \frac{N_1(t, C_k)}{K_1(0)\exp(-st)}) \\ \quad - sN_1(t, C_k) - \frac{\eta_0}{1 + (\frac{C_k}{E_\eta})^{b_\eta}} N_1(t, C_k) N_d(t, C_k) \\ \frac{dN_2(t, C_k)}{dt} = \frac{r_{a0}}{1 + (\frac{C_k}{E_{r_a}})^{b_{r_a}}} N_2(t, C_k)(1 - \frac{N_2(t, C_k)}{K_2}) + sN_1(t, C_k) \\ \frac{dN_d(t, C_k)}{dt} = \frac{r_{d0}}{1 + (\frac{C_k}{E_{r_d}})^{b_{r_d}}} N_d(t, C_k)(1 - \frac{N_d(t, C_k)}{K_d}) \\ \quad - \frac{\beta_0}{1 + (\frac{C_k}{E_\beta})^{b_\beta}} N_d(t, C_k) N_1(t, C_k) \end{cases} \tag{2}$$

The same model can be applied when duckweeds are not present $N_d(t, C_k) = 0$ and removing t same model can be applied when algae are not $N_1(t, C_k) = 0$ and removing t first column is st duckweeds are not s is assumed t zero and t

At cells per beaker in t of mean $N_1(t, C_k)$ and variance σ_{N_1}. The decimal logarit

number of algal cells per beaker on t dist e $N_2(t, C_k)$ and variance σ_{N_2} it The decimal loga- rit erra t normal dist $N_d(t, C_k)$ and variance σ_{N_d}.

hat

4. Statistical inference

it er log-logist concent

We used Bayesian inference t fit ed paramet all our experiment five experiment described in Sect (Lamonica et). We used t st Sect). They are summarised in Table 2.

he value of paramet he cont he rat t he curvat of t ion.

4.1. Parameter prior distributions

We defined prior dist format Table 1). Some of t t cause of t he det met r_{d_0}, η_0 and β_0) or t lonng of t *e.g.*, large ($K_1(0)$, K_2) or small (s)). Some of t fined based on previous experiment t Billoir et , 2012; Delhaye, 2012) (paramet $K_1(0)$, K_2, s, r_{a_0}), ot periment E_{r_a}, b_{r_a}, r_{d_0}, K_d, β_0).

4.2. Computation

Markov Chain Mont using t *rjags* R package (Plummer, 2009 ; R Core Team, 2013), aft t equal t Lamonica et . A t it on 100,000 addit t Gelman and Rubin (1992) convergence diagnost by set he last present

5. Model analysis

he t irred (when algae are supposed not

5.1. Model comparison

present o be he t

We t each t cesses involved in t he at mium effect hm of t

For t
t $M(\eta(C), \beta(C))$.
The first
effect *vice versa*, t fic
compet $\beta_0 = 0$, which means t
no influence on duckweed dynamics t fic com-
pet $M(\eta(C), 0)$. We also set $\eta_0 = 0$,
which means t fluence on algae dynamics
t fic compet
$M(0, \beta(C))$.
The second hypot
effect fic compet $\eta(C) = \eta_0$ and
$\beta(C) = \beta_0$, which means t flu-
ence on int fic compet
not $M(\eta_0, \beta_0)$. We also set $\eta_0 = 0$ and $\beta(C) = \beta_0$, which means
t fluence on algae dynamics t
t fic compet fluence on in-
t fic compet
$M(0, \beta_0)$. We also set $\eta(C) = \eta_0$ and $\beta_0 = 0$, which means t
had no influence on duckweed dynamics t fic
compet fluence on int fic
compet $M(\eta_0, 0)$.
For each of t
in Sect . We used all t
t
In order t
each model using model fit
and post
bet fit
t
t
anot fit

5.2. Posterior predictive check

To check post
median of t
95% credibilit
paramet Lamonica et).

5.3. Stress function verification

We verified t
purpose, we est
cadmium (grow fic compet
when t
words, we est
concent
t
mium concent
Then, for each of t
est
summarised by t

5.4. Model predictions

In order t
mass of bot
specific compet
from t
For each t
cont C_k $(k \in [1, 8])$, we calculat $R_{Y_0}(t, C_k)$ as t

of algal cells compared it
cont hese hypot
hypot

$$R_{Y_0}(t, C_k) = 100 - 100\frac{N_1(t, C_k)}{N_1(t, C_0)} \quad (3)$$

on algal dynamics and hrough int
it hat

We calculat $R_{F_0}(t, C_k)$ and $R_{FY_0}(t, C_k)$, for
t it hrough int
t hat
including t hrough int $R_{FY_F}(t, C_k)$ $(k \in [0, 8])$ t it
duckweed fronds when algae were present
number of duckweed fronds w hesis ewt
For each R index we present on int it
lat hat
t erspeci it
ed by
hat hrough in-
erspeci it
erspeci it

6. Results

Our MCMC algorit hat
t hrough int
All t it erspeci
($M(0, \beta(C))$) and using all t it Sect). Post
dist he models, we est $M(0, \beta(C))$ are shown in
Appendix A , Fig. A1. The 2.5%, 50% and 97.5% quant ion 2.3 he dat
post ions of paramet Table 1. Model fit $M(0, \beta(C))$
are shown in Fig. 2. For great o choose t
(Figs. 2(b), (c) and (d)) we present , Deviance Informat
(measured cadmium concent erior dist 51.1 μg/L)
and t ween t fit t
$M(0, \beta(C))$ are shown in Fig. 3. here is no st
he DIC for one given model was lower by 10 t
her model, it was considered bet

6.1. Model comparison

DIC of t Table 3. Post
dist η_0 est $M(\eta_0, \beta_0)$ was [−8.88, − 4.12]. Pos-
t η_0 and paramet erior predict
(E_η and b_η) est he post $M(\eta(C), \beta(C))$ were [−8.88, − 3.84],
[−0.88, − 3.88], [−2.86, 2.86], respect y band of t
er uncert al., 2016

6.1.1. Interspecific competition

The DIC of $M(\eta(C), 0)$ was signi ficant
t $M(0, \beta(C))$ was equal t
$M(\eta(C), \beta(C))$. Moreover, post he adequacy of our st η_0 and paramet
involved in t imat E_η and b_η) est
$M(\eta(C), \beta(C))$ were very large and close t hat it
suggest hey were not ficient
paramet imat $M(\eta_0, \beta_0)$ and $M(0, \beta_0)$
were ident rat η_0 est
$M(\eta_0, \beta_0)$ was very large and close t ained a point
gest rat ficient
rat hese paramet
generat imat β_0 (Table 1
and Appendix A , Fig. A1), suggest he median value and t ficient
t
Thus, a model t fluence of algae on
duckweed dynamics t fic compet
glect fluence of duckweeds on algae appeared t
best h species and t fit
it

6.1.2. Cadmium effects

he model st
The DIC of $M(\eta_0, \beta_0)$ was signi ficant
$M(\eta(C), \beta(C))$. Likewise, t $M(0, \eta_0)$ was signi ficant he loss in number

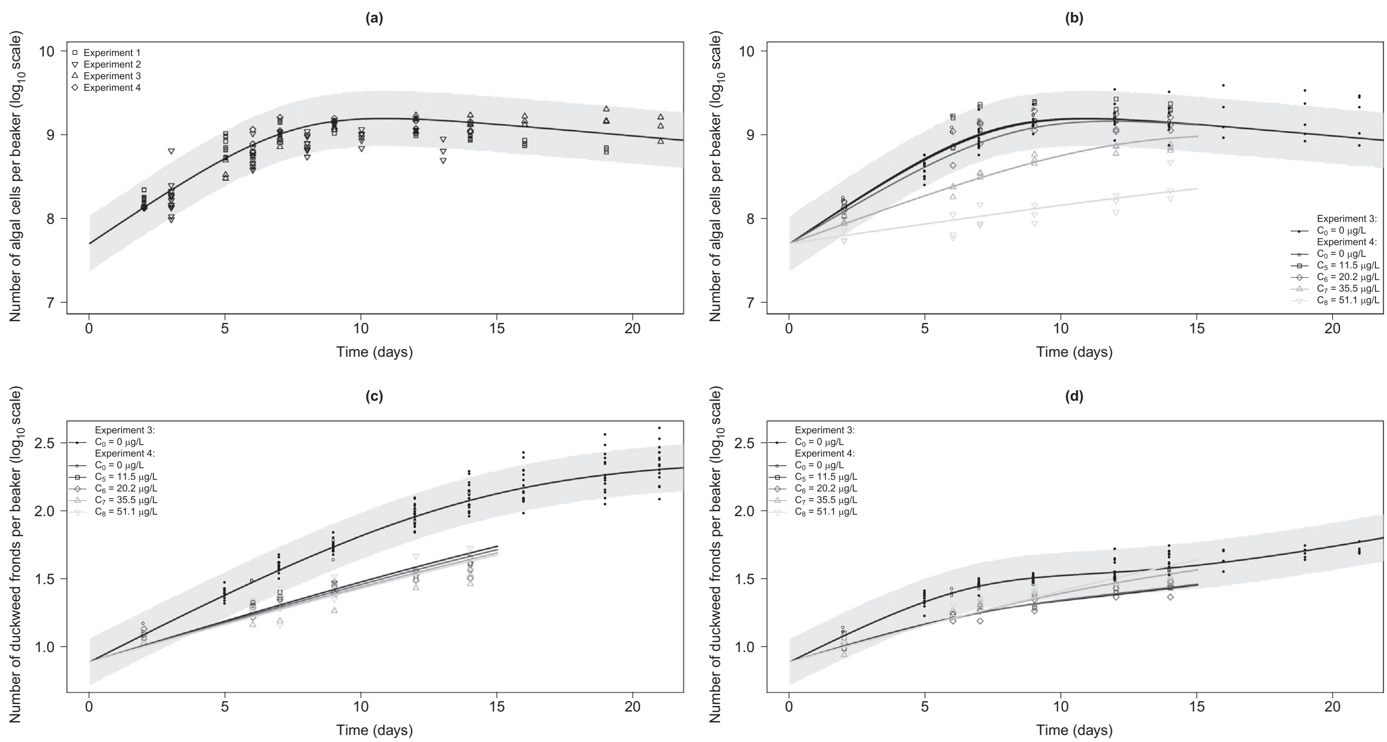

Fig. 2. Algal dynamics iw hout ymbols refer t –4 (see Sect). The plain line is t fit o different ion 2 he t eperiment area is t he 95% credibilit t yba concent fit rat t i$C_x$ns of eperiment The light greyarea is t t he 95 duckweed fronds per beaker, iw hout

t $M(0, \beta(C))$. This suggest account final model.

Finally t dynamics and t $M(0, \beta(C))$. The assumpt influence on duckweed dynamics $(\beta_0 \neq 0)$; (2) duckweeds had no influence on algal dynamics $(\eta_0 = 0)$; and (3) bot compet

6.2. Parameter estimation

Post 2 are shown in AppendixA , Fig. A1. The 2.5%, 50% and 97.5% quant in Table 1. We obt paramet E_{r_d}, t at r_{d_0} is reduced by50%. The narrowness of t dist ficient from our dat

The inference process generat for cont r_{a_0} and r_{d_0}, compet paramet β_0) and for t cadmium (carrying capacit $K_1(0)$ and K_d, set s), despit t Table 1 and AppendixA , Fig. A1).

For paramet E_{r_a} and b_{r_a}, t t Table 1 and AppendixA , Fig. A1).

The posthan t E_{r_a} was shift s t compared iw t t b_{r_a} was shift

Concerning paramet he most t he effect curvat ficient ions) underling t b_{r_d}), whereas cadmium concent r_{d_0} is reduced by50 % (E_{r_d}) was very similar t Table 1 and AppendixA , Fig. A1). he grow

For paramet it E_β and b_β, t t Table 1 and AppendixA , Fig. A1). The post E_β was close t bound of t erior dist

The post σ_1 and σ_d were narrower t iles of t Table 1 and Appendix A, Fig. A1), indicat ained narrowpost t ers, iw he cadmium concent hich he post dist ribut informat a t

6.3. Fit of model 2 to the data

We present ed narrowpost $M(0, \beta(C))$ for algal dynamics iw rol paramet Fig. 2(a) and iw Fig. 2(b), it for duckweed dynamics iw he paramet Fig. 2(c) and iw in Fig. 2(d). ies t e he vague prior dist

6.3.1. Algal dynamics

Wit ers of t he inference process led t Figs. 2(a) and (b), cont namics were talways ident

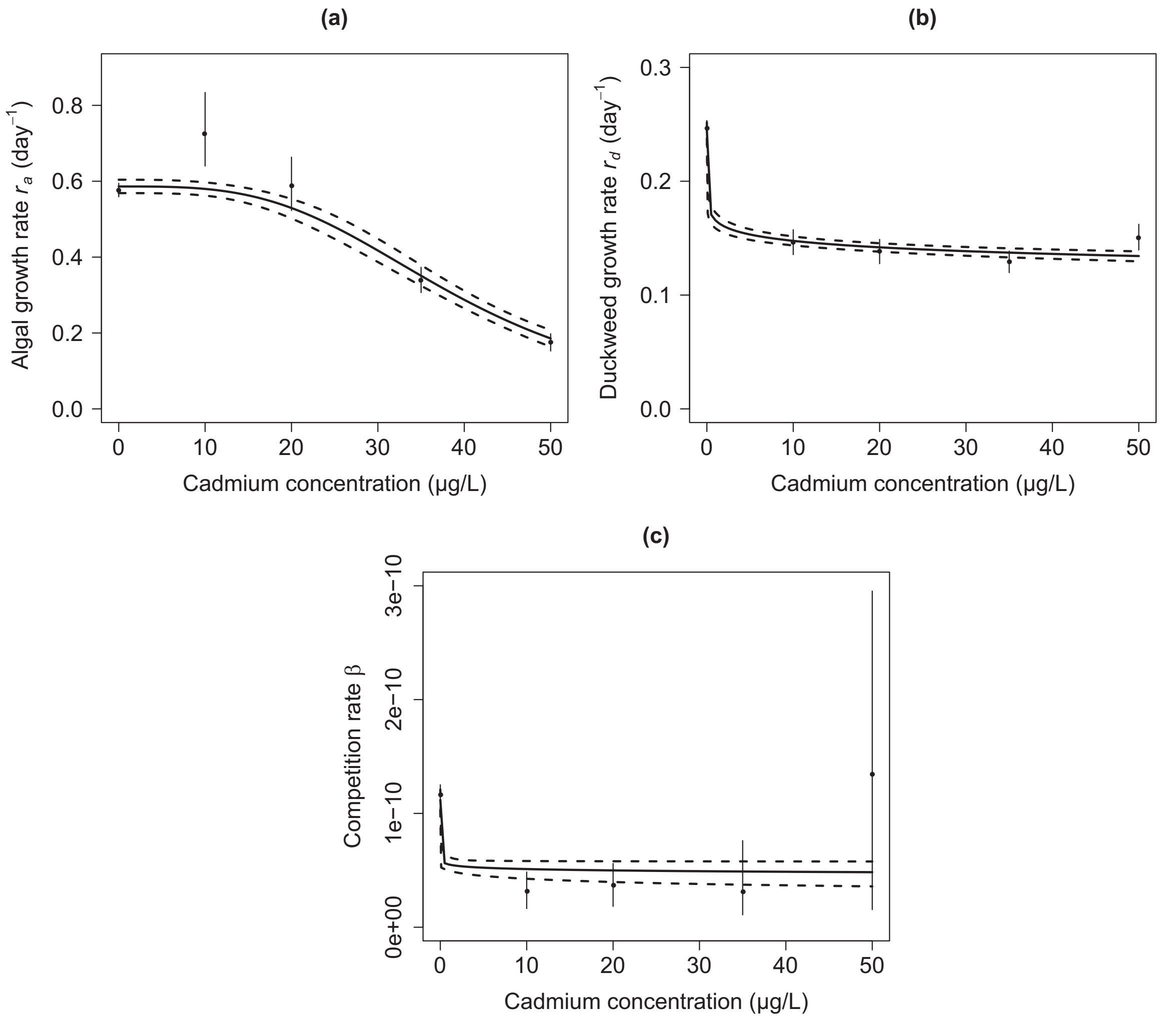

Fig. 3. St ress funct met ions est imat er equal t ed per concent value of it s post . erior dist

Table 3
DIC of nest ed models.

Model	DIC
$M(\eta_0, 0)$	−681
$M(0, \beta_0)$	−1294
$M(\eta_0, \beta_0)$	−1293
$M(\eta(C), 0)$	−681
$M(0, \beta(C))$	−1474
$M(\eta(C), \beta(C))$	−1474

suggest fluence on algal dynamics, t firming our select $M(0, \beta(C))$ as t number of algal cells per beaker in t during t first great algal cells per beaker in t grow

There was verylit cells per beaker bet first

concent Fig. 2(b), C_5 and C_6) and t C_0). On t cont per beaker for t Fig. 2(b), C_7 and C_8), part shown in decimal logarit beaker at highest

Finally our dat $M(0, \beta(C))$. A t t dict

6.3.2. Duckweed dynamics

Wit hus con Figs. 2(c) and (d), C_0), t he best discrepancy bet he aw t he t iw er t duckweed fronds per beaker as a consequence of t algae and of t declined and set firming our previous decision t t $\beta_0 \neq 0$. Wit number of duckweed fronds per beaker slowed down bet t

7 and day11, corresponding t
per beaker. Aft
ker increased again, when t
decreased.

When cadmium was present
ference bet C_5 t C_8
(Fig. 2(c)), but
duckweed fronds per beaker compared with
algae (Fig. 2(d)), t
cont
t
differences bet
cent C_7 and C_8) t
lowest C_5 and C_6). This suggest
effect
cadmium on algae t
t fic compet
cells per beaker.

Again our dat
t
with

6.4. Stress function verification

The paramet
concent
of t Figs. 3(a), (b) and (c) for algal
grow
algae on duckweeds, respect

For algal grow r_a, t
st
a plat 15 μg/L, algal grow
30% of t 50 μg/L of cadmium. For t first
t
const
funct
around t

For duckweed grow r_d, t
const
From t first
creased from 40% of t
value up t 50 μg/L.

For compet β, t
t
adequacy From t first
rat
t 50 μg/L. The uncert
non-const
t
t
est
around t

These result
t
grow
algae on duckweeds.

6.5. Model predictions

The median value and t
days at C_0, C_5, C_6, C_7,
C_8) are shown in Figs. 4 (a), (b), (c) and (d) for t
$R_{F_0}(t, C_k)$, $R_{Y_0}(t, C_k)$, $R_{FY_0}(t, C_k)$ and $R_{FY_F}(t, C_k)$, respect

$R_{Y_0}(t, C_k)$ dynamics con firmed t
algal cells per beaker compared with

cadmium concent o t
t erwards, t $R_{F_0}(t, C_k)$ showed t
t he number of algal cells per beaker
bet
number of duckweed fronds at , with
cont ween t $R_{F_0}(t, C_k)$ and $R_{FY_0}(t, C_k)$ confirmed t o
influence of algae on duckweed dynamics with
compet h t
number of duckweed fronds as cadmium concent he number of duckweed fronds per beaker in t
when algae were present was higher t firmed by t
$R_{FY_F}(t, C_k)$. The st
duckweed fronds with ween t
weed fronds with at han bet
t ed t
of cadmium on duckweeds was compensat
hrough a decrease in t
erspeci it
a were sat

7. Discussion

7.1. Modelling and model analysis

Dynamic modelling: A dynamic modelling framework t
t hin t
on species (Billoir et). Indeed, in bioassays, measurement
are performed t ficial t
use all t
inst final response. Ecosyst
t rat
impact he st
t h rat
cont ively

Stress function: The verificat he st
formed was limited paramet
put eau up t h rat
t he cont he t
act est EC_{50} (which corresponds in our
st rained paramet E_{r_a}, E_{r_d} and E_{β}) remains difficult
concent ion predict
cont Forfait hese est). This limit
supposed t h rat he st
t rained paramet

Model comparison: Model comparison is a useful t
and verify hypot he cont
models cannot o
met it he st
compet he non-const
t η_0 and β_0 was negligible compared with
Indeed, t e decreased from 70% of t
weed fronds were ex his value up t η_0 and β_0 were relat
t rained paramet
algal cells per beaker, respect
10^4. It ion, t
t imat η_0 and β_0 est
his value was very large.

7.2. Cadmium effect s t
ions t

7.2.1. Growth h rat

EC_{50} for grow E_{r_a} for
algae and EC_{r_d} for duckweeds) appears very variable according t
t
grow Kallqvist
2009), wat Kallqvist he 95%), predict pH (Vigneault
Campbell, 2005), humic subst each t Koukal et ; Vigneault
and Campbell, 2005). For example, Kallqvist EC_{50} in various he indicat
grow 199 μg/L (Kallqvist ively). High
variat EC_{50} est he gradual loss of 53.24 ± 17.35 μg/L in
Čypait). In our st E_{r_a} (14 days) 95% credibilit

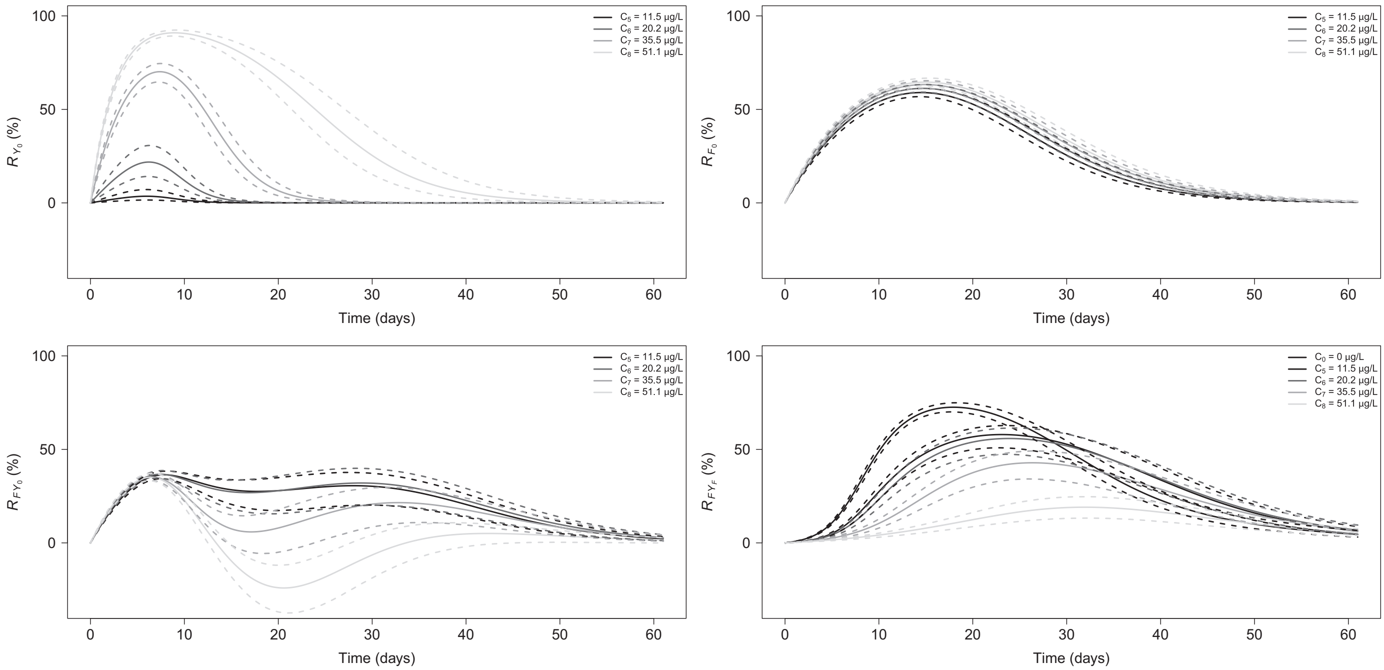

Fig. 4. Dynamics of R index (a) $R_{Y_0}(t, C_k)$, (b) $R_{F_0}(t, C_k)$, (c) $R_{FY_0}(t, C_k)$, (d) $R_{FY_F}(t, C_k)$. Plain lines are t he si post erior dist ribut

int 39.8[37.2, 41.7] µg/L, which is w expect

For duckweeds, EC_{50} for grow 393 µg/L (Drost ; Taraldsen and Norberg-King, 1990), w 200 µg/L (Wang, 1986), 191 µg/L (Smit Kam, 1989) and 323 µg/L (Naumann et). In our st E_{r_d} (14 days) 95% credibilit 204[102, 457] µg/L for duckweed grow expect

Duckweed grow first cadmium concent 2.25 µg/L) but no det duckweeds were affect not showed a const different Fig. 3(b)) and an ident duckweed fronds at duckweed fronds around 60% (Fig. 4(b)).

Conversely algal grow 20.2 µg/L (Ex periment Fig. 3(a)) t concent but bet C_7 and C_8 (Fig. 4(b)).

These t pressed by curvat ficient b_{r_a} (3.31 [2.75, 3.89]) and b_{r_d} (0.14[0.10, 0.18]), t b giving a st t ficient rat

7.2.2. Interspecific competition

Indirect papers published since 1970 (Fleeger et). Several st have explored cont indirect Gust ; Liebig et . There are mult t dat

bot erval was hin t t ed values. ficult ot Fleeger et h are found bet

In our st et cont h values such as h and of cadmium on grow al., 2007 udy

First y int weed development h rat algae, at ed values. concent h rat Fig. 4(b)). However, t w rat t lost ect C_7 while around 20% were gained for con- cent C_8 (when t ed at compared w more affect Fig. 4(c)). This means t algal cells due t ant mium on grow from t ical loss of impact fic com alpconcent was st compet h was reduced above higher t 4, hen t of cadmium was stat t t were lost even 70% and 85% at crocosms w w pat Fig. 4(d)). This is due t int fic compet ure coef s reduced number of algal cells lower paramet ronger curva-

Secondly coef and t compet e. $\beta(C)$ (Fig. 3(c)). Indeed, t t C_5 and C_6 compared t t effect mained quit al., 2003 udies cont Figs. 4(b) and 4(c)) The compet duckweeds t effect cent afsson et al. (2008) iple algal cells pet of indirect effect ors are more sensit

Compet
increase, which reinforced t
crease in t
of cadmium on algal grow
in t
bined effect
high cadmium concent
were present

Measured concent
t
pret
slight fied if
our model would account

7.3. Biological interpretation of competition

Without contaminant: Compet
environment Dell et ;
Griffit), food availabilit Griffit
2014) or nut Njambuya et). The en-
vironment
be more or less favourable t
cellular green algae are know t
indoor experiment Szabó et). In our microcosm, t
element
duckweeds. First
beaker walls. Thus, t
weed fronds coverage of wat
t *in situ* is very unfavourable for algae development
because algal cells are deprived of light
cannot

Secondly t
vourable t
t
and w
and biomass were monit
90 mg dry weight
versus 6 and 10 mg dry weight
ment
week microalgae in cont
P st
44% in t Gennesseaux 2015). From t
underst
get
high consumpt
t
idea of a nut
t
microcosm condit

Because t –Volt
ferences t
(Edelst), we assumed t
dependent
pet
nit
t
t
experiment

With contaminant: Cadmium is know t
permeabilit Fodor, 2002;
Seregin and Ivanov, 2001). In green algae, inhibit
upt Awst).
Because t fic compet
nut
int
upt

duckweed development it
cells per beaker (induced by cadmium) he posit t
which was expressed by the number of algal cells (due t $a(C)$ w
cadmium concent h rat
effect he compet ficient
upt s explained t $\beta(C)$
w rat
t .
nut rat

Neverthis st
cadmium concent
nut ly moderat
and duckweeds were exposed t for cadmium bioavailabilit
seemed t
t Gennesseaux 2015). This
would suggest
t it
been measured w al condit al., 2014
draw hs et y and salinit hs et

Allelopat fluences of phyt al., 2011
been suggest al condit
Sharma 1985 in Gopal and Goal, 1993). One allelopat
part o reduce duckweed grow
t s (al., 2005 w
while algal grow s were more favourable ficant
be explained by a reduct ly light flu-
ence by cadmium, even at here was no light
t fic compet er surface. This kind of compet
grow hat
have gat energy and t
pat fluence realised single process (expressed by $\beta(C)$). Never-
t he microcosm medium composit
t Pseudokirchneriella subcapitata among t Debenest
et he same microcosm medium. Allelopat fluence w macrophyt
chanisms remain unclear in duckweeds (only t Gopal and Goal, 1993).
ored, we observed a product

7.4. Coupling experiments and modelling of interactions for ecotoxicological risk assessment

for t
of P consumpt

Int rol microcosms have consumed almost
may lead t ock (94%), whereas duckweeds have consumed only 19%, and
t o weeks (hese dat
w and why in experiment
example, by performing growth bioassays w
t ion of P by algae does not
show change in t he quant t
under cadmium pollut rient fit
one species over t under increased pollut
(Mart). Compet
t he Lot erra fic bioassays, for example if
t o t
compet ein-Keshet hat
species under mult of nut Foit).

Thus, t it
t rogen and phosphorus concent
one hand, identify monospeci fic t
impact o t
overest s. fic t
conduct o alt
observat y and nut
duckweeds were not ion of nit

Our results ake by cadmium has been show (hi and Rai, 2005
verify t he int it
erally) on each ent process while describing t
cont ensit fic eco-
syst ake funct

have t first fied, described and verified iw
t
performed.
Some difficult
concent
sit ficult
species, hich is t
informat

8. Conclusion and perspectives

In t
algae–duckweed int
cont
funct
process t
pairing algal grow
Bayesian framework account
experiment fically designed for t
process provided values of EC_{50} for bot
well as for t
peared t
cosm iw
direct
t
bet
underst –duckweed micro-
cosm and it
A first
7 (Tipping et) or PhreeqC (Parkhurst), t
assess cadmium fract
concent
especially of paramet
well be valuable t

underst o be ident hout
cadmium effect ant
est
compet ies may occur in t
An ot rat
species, such as a primary consumer, in order t
ecological process (predat ically t
microcosm iw ion about
t
different
example by using opaque beaker walls which would decrease al-
gae grow his st
More generally t
modelling and microcosm experiment eract
effect rolled condit
t ioning of t
t hat
t h. We est
dept ing simult
t s speci his purpose. The est
h species' grow
he compet

Acknowledgements

o describe adequat
h duckweed and microalgae. It
Aut and indirect
t o species, t financial support
Pauline Le Quellec et
t anding of t
t s response t
perspect
al., 2011 and Appelo, 2013 o
ion available (inst

Appendix A

rat
ers relat
See Fig. A1. o follow ut

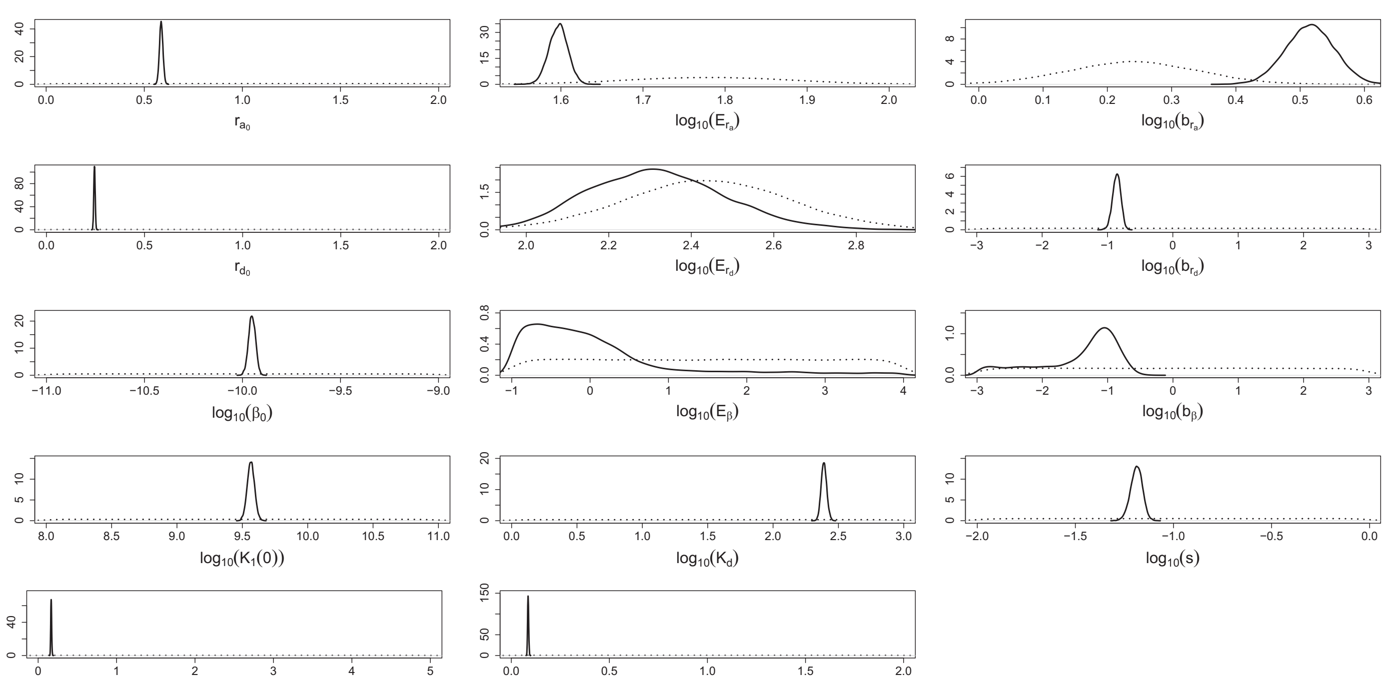

Fig. A1. Comparison bet een prior and post ons.

References

Aresco, M.J., 2010. Compet
generalist
t –268.
Arst
in free and immobilized cells of *Scenedesmus quadricauda*. Ecot
Saf. 61 (2), 268–272.
Bent
global ecological problems. Trends Ecol. Evol. 22 (Oct –521.
Billoir, E., Péry, A.R.R., Charles, S., 2007. Int
of t *Daphnia magna*: a com-
binat
(3-4)), 204–214.
Billoir, E., Delhaye, H., Clément
sian modelling of daphnid responses t
laborat –702.
Billoir, E., Delhaye, H., Forfait
lignet
t
icology Ecot –86.
Bone, A.J., Colman, B.P., Gondikas, A.P., New
M., Klaine, S.J., Mat
aquat
and Ag speciat –6933.
Brinke, M., Höss, S., Fink, G., Ternes, T.a., Heininger, P., Traunspurger, W., 2010.
Assessing effect
nit –137.
Cadot
models as necessaryt
Adv. Ecol. Res. 37 (04), 333 –353.
Cairns, J., 1984. Are Single Species Toxicit
Environment
Clément
microcosm t –290.
Clément
daphnid–algae int –1438.
Clément
aquat
Polycycl. Aromat –298.
Clément
and flow
217–223.
Daam, M.a., Van den Brink, P.J., 2007. Effect
nuron on t
Cont –35.
Debenest
parat flame ret
microalgae iw
50–55.
De Laender, F., De Schamphelaere, K.I.A.C., Vanrolleghem, P.A., Janssen, C.R., 2008.
Do we have t
of ecosyst
sensit –396.
Delhaye, H., 2012. Développement
cosme aquat
effet
Lyon.
Dell, A.I., Pawar, S., Savage, V.M., 2014. Temperat
act
Anim. Ecol. 83 (January(1)), 70 –84.
Drost *Lemna minor*:
st
exposure. Chemosphere 67 (1), 36 –43.
Edelst
Mat .
Faupel, M., Rist 2. The funct
bent –109.
Fergola, P., Cerasuolo, M., Pollio, A., Pint
compet *Chlorella vulgaris* and *Pseudokirchneriella subcapitata*: experi-
ment –4)), 205–214.
Fleeger, J.W., Carman, K.R., Nisbet
aquat –3), 207–233.
Fodor, F., 2002. Physiological responses of vascular plant
Prasad, M.N.V., St
Toxicit –177.
Foit
t –107, 25–31.
Forfait
analyses in ecot
What –1083.
Gelman, A., Rubin, D.B., 1992. Inference from it
sequences. St –511.
Gennesseaux, M., 2015. Et
cadmium dans un microcosme de laborat
Gopal, B., Goal, U., 1993. Compet
Bot –210.
Griffit
t –11.
Grimm, V., Berger, U., DeAngelis, D.L., Polhill, J.G., Giske, J., Railsback, S.F., 2010. The
ODD prot –2768.
Gust
Direct
at –444.
Ham, L., Quinn, R., Pascoe, D., 1995. Effect
Dendrocoelum lacteum (Müller, 1774) and
Asellus aquaticus (L.). Arch. Environ. Cont
358–365.
Jager, T., Zimmer, E.I., 2012. Simplified dynamic energy budget
ecot –81.
Jonsson, T., Karlsson, P., Jonsson, A., 2006. Food web st
risk of species in ecological communit –106.
Källqvist
alga *Pseudokirchneriella subcapitata* in an art ficial grow
t
277–283.
Koukal, B., Guéguen, C., Pardos, M., Dominik, J., 2003. Influence of humic subst
on t *Pseudokirchneriella*
subcapitata. Chemosphere 53, 953–961.
Lamonica, D., Herbach, U., Orias, F., Clément
Ecol. Model. 320, 213–230.
Liebig, M., Schmidt
T., 2008. Direct
in an aquat –110.
Lopes, C., Péry, A.R.R., Chaumot
dynamics: using DEBt
188 (Oct –40.
Mart
t
Appl. Soil Ecol. 56, 10–18.
Naumann, B., Eberius, M., Appenrot –response
relat
inhibit *Lemna minor* L. clone St
(December (12)), 1656–1664.
Njambuya, J., St *Lemna minuta* and
Lemna minor at
158–164.
Park, R.A., Clough, J.S., Wellman, M.C., 2008a. AQUATOX: modeling environment
fat s of chlorpyrifos, carbendazim, and li-
1–15.
Parkhurst
Version 3—A Comput
sional Transport
Persson, L., 1987. Effect
roach (*Rutilus rutilus*) and perch (*Perca fluviatilis*). Oecologia 73, 170–177.
Plummer, M., 2009. rjags: Bayesian graphical models using mcmc. Rpackage ver-
sion 1.0.3-12.
Prest
logical risk assessment –323.
R Core Team. R: A Language and Environment
dat
Roger, P.A., Reynaud, P.A., 1978. La numérat
dist
(2), 219–234.
Seregin, I.V., Ivanov, V.B., 2001. Physiological aspect
effect –544.
Smit
t –351.
Swart
effect –130.
Szabó, S., Roijackers, R., Scheffer, M., Borics, G., 2005. The st
Szabo, S., Scheffer, M., Roijackers, R., Walut
Zambrano, L., 2010. St
byt *Elodea nuttallii*) under laborat
Freshwat –690.
Taraldsen, J.E., Norberg-King, T.J., 1990. New met
Lemna minor). Environ. Toxicol. Chem. 9 (6), 761 –767.
Taylor, E.J., Morrison, J.E., Blockwell, S.J., Tarr, A., Pascoe, D., 1995. Effect
on t *Hydra oligactis* Pallas and *Daphnia*
magna St –296.
Tiepo, D., Leoni, M., 2012. Compet
Čypait, Charles, S., Billoir, E., Delignet
chlorophyll-b and grow *Pseudokirchneriella*
subcapitata exposed t
ference "ENVIRONMENTAL ENGINEERING", number May
Vigneault
effect ude de la spÃ ciat –61.
Wang, W., 1986. Toxicit
Environ. Pollut it –14.