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Environmental and behavioural factors affecting activity in the intertidal gastropod Hydrobia ulvae

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Abstract:

Laboratory microcosms were used to investigate the mud snail Hydrobia ulvae (Pennant) bioturbation activities and behavioural changes in response to snail density, algal food, sediment moisture content, light regime and water cover conditions. Density-dependent kinetics of bioturbated muddy areas were described by von Bertalanffy equations, which provided reliable estimates of mud surface covering rates by snail tracks (m2 h−1 snail−1). Snails need a wet habitat to be active either covered by seawater or by moving in fluid layers for low-tide conditions. Light and microphytobenthic biomass, which are less potent to affect snail activity, are positively interrelated to increase covering rates in the tested chl a concentrations within the range of 1–15 μg g−1. Experimental results suggested us the relevance of microphytobenthos migration processes in affecting crawling activities of H. ulvae that appeared to adjust their foraging efforts in response to benthic algal biomass. Behavioural processes of H. ulvae, in terms of floating, crawling, burrowing and inactive snails, were described using a Markov model. Finally, an empirical model based on von Bertalanffy equations was proposed to describe kinetics of sediment covering by snail tracks under the influences of snail density, sediment moisture content, chl a concentrations and the four combinations of presence/absence of light and seawater. This model should provide a base for further development of a hydrosedimentary model to simulate the effects of H. ulvae bioturbation activities on the resuspension of the intertidal cohesive sediment–water interface for various in situ conditions.

Keywords: Behaviour; Bioturbation; Environmental factors; *Hydrobia ulvae*; Intertidal mudflat; Modelling

1. Introduction

The intertidal habitat is subject to a wide range of rhythmically and rapidly varying features of the environment related to tidal and circadian cycles. In response to these environmental variations, changes in behaviour are common in littoral animals (Palmer, 1987) and especially in the gastropod Hydrobia ulvae (Pennant), which is often reported as the dominant inhabitant of estuaries and intertidal mudflats (Barnes, 1981a; Reise, 1985; Sauriau et al., 1989). Hydrobia ulvae is known to show four modes of intertidal activities (Little and Nix, 1976; Barnes, 1981a): 1) “burying activity”: the snail lies, buried in a small pit just below the sediment surface; 2) “crawling activity”: it crawls across the substratum to feed (in horizontal or vertical plane, in which case this activity was also called “climbing activity”), 3) “floating activity”: it floats within the water column, resuspended by tidal currents or suspended beneath the air/water interface in calm conditions (this last process only takes place after “climbing activity”) and 4) “sinking activity”: it lies inactive on the surface of the sediment. Experimental investigations have suggested that both exogenous and endogenous factors play a part in determining Hydrobia behaviour (Newell, 1962; 1964) as it is the case for other intertidal species (Palmer, 1987). However, studies made by Little and Nix (1976), Barnes (1981a, 1981b and 1986) and Armonies and Hartke (1995) on changes in snail’s behaviour in its natural environment contradicted Newell’s conclusions as they interpreted intertidal activity in terms of crawling/browsing phase when covered by water and an inactive phase when the substratum dries during low tide. No endogenous rhythm could be highlighted. Nevertheless, Hydrobia activities are not so drastically related to the single presence or absence of water cover, as the circadian cycle also affects the activity rhythm of this mollusc (Barnes, 1981b, 1986). Furthermore, snails do not simply crawl when covered by water or remain inactive during low tide, but their 4 behaviour modes occur simultaneously in

natural conditions (except “floating activity” during low tide) and their proportions in crawling, burying, inactive and floating activities may change in response to both tidal and circadian cycles.

Studies undertaken to describe Hydrobia species feeding activities reveal even more complex interrelationships in other environmental and/or biological factors. Grain size (Barnes and Greenwood, 1978; Forbes and Lopez, 1989a), chlorophyll a concentrations (Levinton and Lopez, 1977; Jensen and Siegismund, 1980; Lopez and Cheng, 1983; Bianchi and Levinton, 1984; Forbes and Lopez, 1986; Morrisey, 1988), bacteria populations (Lopez and Cheng, 1983; Bianchi and Levinton 1984), snail density (Levinton and Lopez, 1977; Levinton, 1979; Lôpez-Figueroa and Niell, 1987; Morrissey, 1987; Blanchard et al., 2000) and larval trematodes infection (Mouritsen and Jensen, 1994) are the main factors controlling ingestion, assimilation or growth rates. Hydrobia species also show marked preferences for fine sediments (Barnes and Greenwood 1978), for enriched chlorophyll a sediment (Forbes and Lopez, 1986) and they are attracted to light (Newell, 1962). Since Hydrobia species crawling velocity decreases while their feeding rate remains constant (Forbes and Lopez, 1986), these two separate parameters are not subject to environmental conditions in the same way. However, all the aforementioned factors controlling feeding activities could be involved in controlling covering rates and behavioural activities, as snails need to crawl during feeding.

Variations in Hydrobia ulvae motile activities could have several implications in the ecology, population dynamics and habitat features of this species. For example, distribution patterns, dispersal and recruitment of the population are directly affected by the occurrence of floating behaviour, and Armonies and Hartke (1995) predicted the routes of dispersal of Hydrobia ulvae by the use of a hydrographic model. Secondary production is also directly affected by all factors influencing crawling and feeding activities (Bianchi and Levinton, 1984; Sola, 1996; Lillebø et al., 1999).

Hydrobia ulvae bioturbation activities influence sediment resuspension (Andersen, 2001) and these activities are directly related to bulk sediment properties and especially sediment moisture content (Orvain et al., in prep.). In an attempt to develop a model simulating variations in bioturbation activities under the influence of sediment properties, we performed several series of experiments to assess 1) the influence of moisture content and other environmental factors (i.e. cover by seawater, presence or absence of light, and chlorophyll a concentrations) on sediment covering rates by snail tracks by measuring crawling kinetics in microcosm experiments and 2) the effect of these factors on behavioural processes by measuring the varying proportions of crawling, burying, inactive and floating snails during the same experiments.

The modelling approach was further performed using the following 3 steps: 1) assuming that the covering of sediment surface by tracks produced by crawling snails is a time- and snail density-dependent process sediment, covering rates were quantified in all experiments by fitting a Von Bertalanffy model to experimental crawling kinetics, 2) a simple Markov model was developed to simulate behavioural processes and variations in proportions of crawling, burying, inactive and floating snails during the same experiments, and 3) the effects of behavioural processes on crawling activities were assessed by testing whether a better fit to experimental crawling kinetics could be obtained by applying correction to include active snail densities that were provided by the behaviour model.

2. Material and methods

2.1. Experimental design

The whole experimental set followed a five-way factorial design with replication (n=3), in which snail density, sediment moisture content, chl a concentration, cover by

seawater and presence or absence of light were fixed factors. Due to replication (n=3), tests of 3 snail densities (1,000, 5,000 and 10,000 snails.m^{-2}), 3 sediment moisture contents, 2 chl a concentrations (sediment enriched and non-enriched in diatoms) and 2 water cover regimes (with or without water), a total of 108 microcosms were used in 2 experimental sets (with and without light).

2.2. Experimental procedure

Mud was collected on the Montportail-Brouage mudflat (Marennes-Oléron Bay), brought back to the laboratory, sieved (1 mm) to remove macrofauna and homogenised. Full details on the sediment characteristics at the sampled site were in Gouleau et al. (2000). Mud mixture was diluted with sea water (salinity ca. 31‰), in order to obtain homogeneous sediment moisture content (g water/ g dry sediment×100) of 106%, 225 % and 382%. These values are usually found on the Brouage mudflats (Gouleau et al., 2000). Sediment moisture contents were calculated by weight difference between fresh and dried sediment (for 72 hours at 60 °C).

As for diatom-enriched sediment, it was first necessary to isolate the epipelic algae from the mud to form a suspension, which was then added to the sieved sediment. Epipelic diatoms, which are motile microalgae exhibiting an endogenous rhythm of vertical migration were isolated from the mud. The mud was evenly spread in a tray and covered with a 63-µm net. After 24-36 hours (at low tide) under artificial light, epipelic diatoms had migrated through the net and accumulated in the net. Diatoms were then collected in sea pre-filtered (GF/F filters) water and diatoms were left to settle for 1 hour. The seawater was then thrown away and the algal suspension was then mixed with sieved sediment and used for adjusting sediment moisture content.

Microphytobenthos biomass from enriched and non-enriched sediment were assessed using chl a concentrations. Pigments were extracted from freeze-dried sediment in methanol (80%) for 1 hour in the dark at 4 °C. Fluorescence of the supernatant (after centrifugation) was measured using a Turner Fluorometer and total chl a was calculated according to Lorenzen (1966). Chl a concentrations were equal to 1 and 15 $\mu g.g^{-1}$ for non-enriched and enriched sediments, respectively.

108 microcosms (9 cm in diameter) were filled with prepared mud (6 cm in height) and placed in 2 tanks kept in a 17 °C regulated room. One of the 2 tanks was filled with seawater (salinity ca. 31‰) and the other tank had no seawater in it, to simulate high and low tide, respectively.

The first experimental set was performed in constant darkness and readings were taken with the aid of a standard white-light torch, the light from which was shown not to affect snail behaviour (Barnes, 1986). The second experimental set was performed with a homogeneous artificial light to avoid a strong source of light that could attract snails and influence their behaviour (Newell, 1962).

Crawled areas were measured by two observers over a total period of 24 hours, during which readings were taken at different intervals (after 5, 20, 40 and 60 minutes, thereafter at every hour for 20 hours and finally after 24 hours). Readings were taken frequently at the beginning of experiments, when snail tracks were produced rapidly, but time interval between readings was lengthened at the end of experiments, once whole microcosm areas were bioturbated (i.e. covered by snail tracks). Results were expressed in bioturbated surface relative to the total microcosm surface and maximal values were 100 %. Bioturbated surfaces were measured by using an evaluation scale of surface covered by tracks (1, 2, 5, 10, 15, 20, 30, 40, 50, 75 and 100 %). This evaluation scale (Fig. 1) was elaborated with a picture analysis software (IMAGE-IN).

A number of Hydrobia ulvae were counted on several occasions over the first four hours of experiments (after 5, 10, 20, 30, 60, 120, 180 and 240 minutes). Results were expressed in crawling, floating, sinking and burying snail densities relative to total snail densities. Only microcosms with 5,000 snails.m^{-2} were chosen for these measurements, but all 3 replicates and 4 other environmental factors were kept in the experimental design to test the influence of environmental conditions on behavioural processes.

2.3. Crawling model development

It was hypothesised that the increase in snail density and activity time would increase the probability that snails create new tracks. Bioturbation kinetics, related to crawled areas (i.e. tracks are called T in the model and T is expressed in m^2), are thus dependent on snail density (n in snail.m^{-2}), activity time (t in hours), individual mud surface covering rate by snail tracks (a in $m^2.h^{-1}.snail^{-1}$) and the probability that a snail meets an old-formed track (P no unit).

$$\frac{dT}{dt} = a.n.(1-\mathrm{P}).S \qquad (1)$$

All notations used in all models are synthesised in Table 2. The individual mud surface covering rate by snail tracks (in $m^2.h^{-1}.snail^{-1}$) will be further called “covering rate” and it is defined as the individual crawling velocities (in $m.h^{-1}.snail^{-1}$) multiplied by the track width (in m).

As experimental crawled areas were expressed relative to the whole surface (S in m^2), we converted crawled areas from T in m^2 to ϕ in % :

$$\frac{d\phi}{dt} = a.n.(1-\mathrm{P}) \qquad (2)$$

The probability that a snail meets an old-formed track during a small time interval (Δt) is directly dependent on the surface covered by tracks relative to the total microcosm surface. So, we formulated this probability as follows :

$$P = \frac{T}{S} \quad \text{or} \quad P = \frac{\phi}{100} \tag{3}$$

Consequently, Eq. 2 was transformed into :

$$\frac{d\phi}{dt} = 100.a.n.\left(1 - \frac{\phi}{100}\right) \tag{4}$$

By solving Eq.4, we obtained :

$$\phi = 100.\left(1 - e^{-a.n.t}\right) \tag{5}$$

Such analytic expressions are largely used in marine ecology and especially in population dynamics to describe individual or population growth. For minimisation tests, Eq. 5 that included population covering rates (a_P in $m^2.h^{-1}$) instead of individual covering rates (a in $m^2.h^{-1}.snail^{-1}$) was also used :

$$\phi = 100.\left(1 - e^{-\frac{a_P}{S}.t}\right) \tag{6}$$

Such a model is classically called a Von Bertalanffy model, which are usually used to describe population growth (Barnes and Hughes, 1999; Ebert, 1999).

2.4. Behaviour Markov model development

Markov models have been used widely in ecology for many decades to describe changing states e.g. the influence of deposit-feeders on the burial and transport of sedimentary particles (Jumars et al., 1981), animal behavioural processes (Castro et al., 1992), animal distribution and settlement (Pineda and Caswell, 1997) and animal migrations (Matis et al., 1992).

A Markov model was therefore developed to describe the exchange of snails between the 4 behavioural modes. This simple model contains 4 states : 1) inactive snails, 2) burying snails, 3) crawling snails and 4) floating snails. Expressions that are used in the model to describe proportions of snails occupying these 4 states are I, B, C and F, respectively. The

transition matrix contains 4^2=16 transition probabilities that snails change in behaviour. This number of probabilities has been reduced by only considering changes in behaviour that really occurred during experiments. All snails were inactive at the beginning and some started crawling crawled (t_{IC}). When animals crawled, some climbed on microcosm slides, where they could reach the air-water interface and float (t_{CF}). Some floating snails fell through the water column and over the sediment where they lay inactive (t_{FI}) before crawling again. On fluid layers, some active crawling snails buried themselves in a small pit (t_{CB}). Other changes in behaviour were not observed when snails were submerged and all corresponding probabilities were nil. So, the state (A) and transition (Ω) matrix were :

$$A = \begin{bmatrix} I \\ C \\ F \\ B \end{bmatrix} \qquad \Omega = \begin{bmatrix} -t_{IC} & 0 & t_{FI} & 0 \\ t_{IC} & -(t_{CB}+t_{CF}) & 0 & 0 \\ 0 & t_{CF} & -t_{FI} & 0 \\ 0 & t_{CB} & 0 & 0 \end{bmatrix} \qquad \frac{dA}{dt} = \Omega.A \qquad (7)$$

The Markovian first-order assumption that transition probabilities only depend on the present state and not on the history of past states that snails have occupied, was respected in this application. The additional Markovian assumption that the transition probabilities remain constant over time may not entirely be satisfied because experimental data revealed that floating snail proportions showed maximal values during the first sequences before falling to equilibrium state. Transition probability that floating snail may lie inactive (t_{FI}), remained low during first sequences and then finally increased to become constant over time. This hypothesis allowed us to consider variations in floating behaviour proportions. A logistic equation in function of activity time was chosen to describe this feature :

$$t_{FI} = \frac{k_{FI}}{1 + e^{-\alpha_{FI}(t - t^0_{FI})}} \qquad (8)$$

where k_{FI} is the upper limit of transition probability, α_{FI} is the rate of increase and t^0_{FI} is a time constant of integration defining the position of the curve relative to the origin.

215 The number of probabilities was reduced for experiments without seawater, because
216 the floating behaviour did not exist in such conditions. Furthermore, some burying snails
217 came back to the air-sediment interface during experiments (t_{BC}). In the present case, the
218 model (Eq. 7) was modified as follows :

219 $$A = \begin{bmatrix} I \\ C \\ B \end{bmatrix} \qquad \Omega = \begin{bmatrix} -t_{IC} & 0 & 0 \\ t_{IC} & -t_{CB} & t_{BC} \\ 0 & -t_{BC} & t_{CB} \end{bmatrix} \qquad \frac{dA}{dt} = \Omega.A \qquad (9)$$

220

221 2.5. Model fitting

222 We used an iterative non-linear least squares regression according to Nelder-Mead
223 simplex method to estimate parameter values (Nelder and Mead, 1965). As for Von
224 Bertalanffy and logistic models, differential equations were analytically integrated for
225 computing and minimising. As for the behaviour models, the Markovian matrix were
226 expressed as a system of 4 differential equations, which were integrated numerically using a
227 standard implementation of the fourth-order Runge-Kutta method. As for the Von Bertalanffy
228 models including crawling snail densities rather than total snail densities, all differential
229 equations were integrated numerically using the same method.

230 The calculations of covering rate values and standard errors were made separately for
231 each replicate (n=3) of crawling kinetics. Analyses of variance of covering rates were
232 performed by using these estimates with the MINITAB software. The variance-covariance
233 matrix of final parameters was calculated using a bootstrap method.

234

235 **3. Results**

236

237 3.1. Measurement of crawling kinetics

Crawled areas (Figs. 2 and 3 for respective lit and dark conditions) increased with activity time to converge towards a maximal value of 100% (i.e. when the total surface was covered by tracks). For cases where kinetics were low, the maximal value was not reached in the 24-hour experimental period. The higher the snail density was, the faster the crawling kinetics were for each experiment (Figs. 2 and 3). Crawling activities were thus time- and density-dependent.

In all experiments (Figs. 2 and 3), kinetics were faster when snails were covered by seawater. Snails were also more active on fluid mud (W=225 % and W=382 %) than on compact mud (W=106 %). The other 2 tested factors (i.e. chl a concentrations and light regime) do not seem to affect results as much. However, snails often crawled more slowly on non-enriched sediment than on enriched sediment and more slowly in total darkness than in laboratory-lit conditions.

3.2. Crawling model parameter estimation and variability analysis

Firstly, minimisation tests were performed to 1) ascertain the correctness of model fittings to experimental data, 2) ascertain the correctness of Eq. 5 to describe snail density effects and 3) guarantee reliable calculations of covering rates (a in $m^2.h^{-1}.snail^{-1}$).

We tested Von Bertalanffy models (Eq. 6) on all separate data sets. Since several crawling kinetics seems to follow a logistic curve rather than Von Bertalanffy curves, logistic equation was also tested in our parameter minimisation tests. The formulation of this logistic equation was :

$$\phi = \frac{100}{1 + e^{-\frac{\alpha_P}{S}(t - t^P_{50})}} \quad (10)$$

where α_P is the population crawling rate (α_P in $m^2.h^{-1}$) and t_{50} is a constant of integration defining the position of the curve relative to the origin.

Due to the test of 3 snail densities, 3 sediment moisture contents, 2 chl a concentrations, 2 degrees of water cover and 2 light regimes, 72 separate models were adjusted to pools of replicated series of 22 observations (n=3×22=66). For Von Bertalanffy (Eq. 6) and logistic (Eq. 10) models, 72 population covering rates (α_P and a_P) were estimated, but for logistic models, an additional set of 72 parameters (t^P_{50}) was minimised. Both models provided good fittings with a better accuracy obtained by logistic models (r^2=0.962) compared to Von Bertalanffy models (r^2=0.943; $F_{72,4606}$=38.82; p=0).

The results of our present study agreed with those of Lôpez-Figueroa and Niell (1987), in experiments which involved long-term periods (3 days). A direct comparison of our results to their results (Fig. 4) was proposed for experiments in which the combination of environmental conditions was similar (i.e. with 10,000 snails.m^{-2} on the most compact sediment, which was enriched in live or dead diatoms in the presence of light and seawater). We compared fitting Eq. 6 separately to our data series and to their data series (with independent parameter value estimates) to fitting the equation to our data gathered with their data (with a single parameter value estimate). Fitting separate models (r^2=0.858) did not provide a significantly better fit than fitting the gathered series model (r^2=0.925; $F_{1,194}$=2.85; p=0.092). This result demonstrated that our experimental procedure provided reliable measures that could guarantee satisfactory and similar results irrespective of observers and areas from which snails are taken.

Parameters of Eq. 5 were therefore estimated by fitting to experimental results to describe snail density effect. Logistic models were also tested in this minimisation test and Eq. 10 was modified to include the snail density (n) and the individual covering rate (α) as follows:

285 $$\phi = \frac{100}{1+e^{-\alpha.n.(t-t_{50})}} \quad (11)$$

286 24 parameters (i.e. a expressed in $m^2.h^{-1}.snail^{-1}$) were estimated for Von Bertalanffy
287 models instead of 48 parameters (i.e. α and t_{50}) for logistic models. Von Bertalanffy models
288 were more suitable to include snail density influence, as a significantly better fit (r^2=0.914)
289 was yielded by these models compared to logistic models (r^2=0.760). Covering rate estimates
290 with their standard errors are synthesised in Table 2.

291 Secondly, minimisation tests were performed to establish an equation describing
292 sediment moisture content and chl a concentration influences on covering rates and
293 bioturbation kinetics. Covering rate estimates were dressed in function of sediment moisture
294 content and chl a concentration (Fig. 5) for the 4 combinations of light regime and water cover
295 (i.e. in presence of seawater and light – in presence of seawater and in absence of light – in
296 absence of seawater and in presence of light- in absence of seawater and light). Covering rate
297 variations (Table 2) confirmed influences of environmental conditions on bioturbation
298 kinetics with significant effects of all 4 tested factors (2 four-way ANOVA on lit and dark
299 experiments; *p<0.05). They remained nil whatever the sediment moisture content and chl a
300 concentration when exposed to darkness without seawater and they were also nil for compact
301 mud in lit conditions without seawater, but increased in function of sediment moisture content
302 by following an exponential curve. In lit conditions and in presence of water, covering rates
303 were also higher for diatom enriched sediment. When snails were submerged, covering rates
304 always followed a sigmoid pattern in function of sediment moisture content and their values
305 were lower on a diatom non-enriched sediment in diatoms when exposed to darkness.
306 Sediment moisture content and chl a concentration were included as compound equations in
307 Eq. 5 to simulate their effects on covering rates without modifying snail density and activity
308 time influences (Fig. 5) :

309 $$\phi = 100.\left(1 - e^{-a.n.t}\right) \quad \text{with} \quad a = a_0 . f(w).g(chla) \tag{12}$$

310 All constant and parameters of these equations and others are synthesised in Table 1.

311 We used no fundamental idea taken from previous studies about the way of including
312 these variables in our mathematical formulations. The model was thus built on the basis of the
313 analysis of our results, in order to simulate positive influences of sediment moisture content
314 and microphytobenthic biomass. The influence of sediment moisture content on bioturbation
315 activities was assessed by Orvain et al. (in prep.) in terms of resuspended sediment, and
316 especially, in terms of sediment mass (in $g.m^{-2}$) produced by snails within a "biogenic matrix"
317 that is easily resuspended. Such a process can provide tools for finding a reliable
318 mathematical formulation. These experimental results revealed an exponential increase of this
319 amount in function of sediment moisture content within the range of 150-300 %. Since direct
320 mathematical links occur between crawling surfaces and bioturbated sediment mass amount
321 (Orvain, unpublished), we can suggest an exponential expression of covering rates versus
322 sediment moisture content. The f(W) equation compound (in Eq. 12) that represented effects
323 of moisture content for formulation of covering rates, was thus expressed as follows :

324 $$f(W) = e^{\gamma W} \tag{13}$$

325 This equation provides an exponential response of covering rate in function of sediment
326 moisture content and such a response was suitable to describe our results without seawater
327 (Fig. 5a and 5b). However, analysis of results obtained in presence of seawater (Fig. 5c and
328 5d), suggested a sigmoid curve rather than an exponential curve as a plateau was reached for
329 sediment moisture content close to 382 %. Hence, Eq. 13 was therefore transformed into a
330 sigmoid equation :

331 $$f(W) = \frac{1}{1 + e^{-\eta(W - W_{50})}} \tag{14}$$

Chl a concentration effects (Fig. 5) were more pronounced in compact mud (W=106 %) than in fluid mud (W=285% or W=382 %) in high tide experiments, unlike low tide experiments. This complex interaction between sediment moisture content and chl a concentration should appear in the mathematical equation of covering rates. Several combinations of these two variables were tested in several equations in order to perform minimisation tests and to retain the combination, which was the most adjusted to our experimental data:

$$g(chla) = e^{chla^{\lambda/W}} \quad (15)$$

With a set of 4 independent value parameter estimates (W_{50}, λ,η and a_0) for each case (i.e. in presence of seawater and light – in presence of seawater and in absence of light – in absence of seawater and in presence of light- in absence of seawater and light), both Eqs. 14 and 15 yielded good fits to crawling kinetics (r^2=0.899). By searching for a set of commune parameters to fit to all experimental results without reducing the accuracy guaranteed with a set of 4 independent values for each of the 4 parameters too much, we retained a model with 4 individual estimates of W_{50} and a_0 and commune estimate of λ and η (r^2=0.883; $F_{6,4734}$=128.28; p=0). Parameter estimates are synthesised in Table 3 and the computed results of estimated covering rates versus chl a concentration and sediment moisture content were drawn in Fig. 8. Whatever were the conditions, maximal covering rates were reached for the sediment moisture content ca. 200 %.

3.3.Measurement of behavioural processes

Percentages of crawling, floating, sinking and burying snails were highly variable during the experimental period (Figs. 7 and 8 for respective lit and dark conditions). All snails were inactive at the beginning of experiments when we put them in microcosms and they

356 reacted more or less rapidly (sometimes within 1 minute), according to whether they found the
357 necessary conditions to make them active. Subsequently, very large proportions of snails
358 crawled at the beginning of the sequence. Flotation, which is an accidental passive event after
359 climbing (Barnes, 1981a), only appeared after this crawling phase, during which they covered
360 the distance to air-water interface. Tendencies of the snails to float were then marked during
361 the first hour of the sequence and, as a result, tendencies of the snails to crawl were inversely
362 marked during the same time. The duration of this floating period was variable according to
363 conditions. Newell (1962) and Barnes (1981a) observed similar patterns for floating snails and
364 for climbing snails, respectively. After this period, proportions of crawling snails increased
365 while proportions of floating snails reduced, until both crawling and floating proportions
366 reached a constant suggesting an equilibrium state.

367 As obtained for bioturbation kinetics, behavioural activities were affected by variations
368 in the 4 tested environmental factors with interrelated influences. Large proportions of snails
369 crawled when they were in a wet habitat (e.g. when covered by seawater and on fluid layers
370 for low tide experiments). On compact mud (i.e. W=106%), all snails remained inactive on
371 dried sediments (i.e. without seawater), except in one special case, in which snails were
372 subjected to constant darkness on a chl a enriched sediment. Several authors reported such
373 inactivity, when animals are placed in a dried environment (Newell, 1962; Little and Nix,
374 1976; Barnes, 1981a).

375 Comparison of Figs. 7 and 8 revealed that the influence of light regime is a complex
376 feature: when covered by seawater, much larger proportions of snails crawled when they were
377 exposed to darkness rather than light, except when they were covered by seawater on a chl a
378 enriched sediment, in which case most snails were floating. However, differences in
379 proportions of inactive animals between experiments in the presence or absence of light was
380 not observed when submerged. Influence of light on crawling densities were similar without

seawater, except in one experiment (i.e. on chl a enriched compact mud) in which animals were more active when they were exposed to constant darkness than laboratory-lit conditions.

In the absence of seawater, the enrichment of sediment in benthic diatoms made the proportions of active snails increase. Such an influence was not observed when snails were submerged.

3.4. Behaviour model parameter estimation and variability analysis

The last step of minimisation tests consisted of the behaviour model development and of testing whether crawling models could be improved by incorporating behavioural processes. 12 t_{CB}, t_{IC}, t_{CF}, k_{FI}, t^0_{FI} and α_{FI} (Eqs. 7 and 8) parameter sets were separately estimated to fit to each of the 12 data series of relative snail numbers for experiments performed with seawater (Figs. 7 and 8). 12 t_{IC}, t_{CI}, t_{CB} and t_{BC} (Eq. 9) parameter sets were separately estimated to fit to each of the 12 data series (with 24 data points) of relative snail numbers for experiments performed without seawater (Figs. 7 and 8) . Behaviour models were better fitted for experiments with seawater (r^2=0.925) than without seawater (r^2=0.771).

These behaviour models (Eqs. 7, 8 and 9) were therefore combined with the Von Bertalanffy crawling models (Eq. 4) to include varying crawling snail densities as variables in Eq. 4 instead of total snail densities (n). This correction did not provide a better fit (r^2=0.913 instead of r^2=0.914). Corrected individual covering rate estimates are presented with their standard errors in Table 2. Incorporation of behavioural processes always increased crawling snail estimates (Table 2) and variations in the 4 tested factors still affected covering rates in a similar way for both experimental sets with or without light (2 four-way ANOVA on lit and dark experiments, ***$p<0.001$). No further behaviour model development was performed

since behavioural processes did not contribute to a significant reduction in the residual sum of squares when fitting Von Bertalanffy models.

4. Discussion

4.1 The choice of the Von Bertalanffy model

The Von Bertalanffy model (Eq. 5) is the most suitable model to describe snail density effects on crawling kinetics because it was built taking into accounts theoretical backgrounds about probabilities that snails met old-formed-tracks. Since some curves (Figs. 2 and 3) seem to follow a logistic pattern, logistic models were also tested to describe snail density effects and logistic models (Eq. 10) indeed guaranteed better fit than Von Bertalanffy models (Eq. 6) when adjusting to the 72 separate data sets. However, Von bertalanffy models (Eq. 5) were much better adjusted to our experimental data than logistic models (Eq. 11) to include the snail density as a variable in models. Moreover, Von Bertalanffy models have the advantage to include one single parameter (i.e the covering rate) in their equations whereas an additional paramater (i.e. t_{50}) is necessary in logistic models.

Blanchard et al. (2000) formulated a random walk model considering behavioural processes in order to simulate the density-dependence of ingestion rate. One of the tested hypotheses was that snails may create mucus tracks which prevent other snails from eating microphytobenthic cells. They rejected this assumption as they found contradictory results to their experimental data. In our present case, the model was developed to simulate bioturbation kinetics, and the latter hypothesis is reliable as old-formed tracks prevent other snails to form new tracks in this local area. For a simplicity's sake, we preferred the Von Bertalanffy analytic model to their random walk model, since this model has been established for parameter minimisation by comparing computed results to experimental results. For further use of this

model, analytic formulation will also allow quick and accurate calculations of covering rates and is thus preferable.

By estimating the snail track width within the range of 500-1000 µm and by using the maximal covering rate ca. 2.10^{-4} $m^2.h^{-1}.snail^{-1}$ (Table 2), we can propose an estimate of individual crawling rate within the range 0.33-0.66 $cm.mn^{-1}$. These values are close to those estimated by Mouritsen and Jensen (1994) and Forbes and Lopez (1986) who found individual covering rates equal to 0.5 $cm.mn^{-1}$ and 0.2 $cm.mn^{-1}$ respectively on submerged fluid sediments with low chl a concentrations.

4.2 Water presence effects

In our experimental conditions, all snails were active in less than 5 minutes when covered by water, whatever the light regime (Figs. 4 and 5). Without seawater, the probabilities that inactive snails began crawling were directly dependent on sediment moisture content (Figs. 4 and 5). Barnes (1986) concluded that “of the two variables, the absence of light is therefore more potent in influencing activity than is the presence of water cover”. In our experiments, water cover and sediment moisture content influences on active snail densities and on covering rates revealed that the presence of seawater is a necessary condition for snails to become active. Chl a concentration and light affected snail activities to a lesser extent by stimulating snails, once they were already active. Barnes (1986) damped the sediment and modified sediment moisture contents while carrying out his experiments. He thus minimised the influence of water presence that should occur in natural low tide conditions.

4.3 Microphytobenthic biomass effects

As all our experiments, where snails could be active (i.e. for moistened sediments), covering rates were positively influenced by chl a concentrations within the range of 1-15 $\mu g.g^{-1}$ (Fig. 5). Conversely, Forbes and Lopez (1986) observed a decrease in covering rates versus chl a concentrations within the range of 51-108 $\mu g.g^{-1}$. In another study, however, Forbes and Lopez (1989a) found a decrease in locomotion activities with chl a concentrations by comparing sediment processing rates between different silt-clay sediments. Their results of sediment processing rates were 94, 133 and 141 µg sediment.h^{-1} for respective chl a concentrations of 68, 82 and 202 $\mu g.g^{-1}$. However, comparison among their experimental results was debatable because sediment and snails were taken from different sites in each case. We could suggest that snails adjust their foraging effort in response to microphytobenthic biomass. Indeed, opposite conclusions between Forbes and Lopez (1986) and us could be interpreted in terms of individual energetic costs and in terms of optimal foraging strategy, which could be different according to food density. A lot of predators and deposit-feeder species react to variations in prey density by increasing their individual feeding activities as their motive activities, until reaching an optimal feeding rate (Holling, 1959; Taghon and Jumars, 1984; Abrams, 1992). According to this theory, animals can decrease their motive activities while maintaining their feeding rate constant for values greater than this threshold. As a result, an increase in relative prey densities entails a gain in net energy gained per day (net gains = gross caloric intake – total daily caloric expenditure), either by increasing consumed energy with an increase in feeding and motive activities or by decreasing losses in energy by reducing motive activities while maintaining the consumed energy constant. Such an assumption, which means that animals are likely to maximise their net intake of energy, either by cost minimising or by maximising energy over the course of each day, depending on diatom biomass, can help us to understand our results which are apparently opposite to Forbes and Lopez's results. Kofoed (1975) showed that energy involved in pedal mucus production is

not negligeable for Hydrobia species and represents 9 % of total assimilated energy. Accordingly, Taghon (1982) developed an optimal foraging model, which predicted that ingestion rates and food values should co-vary positively in order to maximise net time rate of energy gain. Model predictions were supported by experiments performed with three deposit-feeding polychaete species (Taghon and Jumars, 1984). Our interpretations and data involving crawling activities also support these model predictions.

Forbes and Lopez (1989a) demonstrated that feeding rates of microalgal carbon were higher on sand than on silt-clay. Microalgal concentrations were lower in sand than in silt-clay (4 compared to 68 $\mu g.g^{-1}$). They interpreted their results by suggesting that Hydrobia species may have to crawl more on sand in order to meet their daily nutrient requirement since food is less concentrated in coarse sediments. Snails process many more sediments when feeding on sand rather than on silt-clay. This is accomplished by a switch in feeding mode, from particle swallowing to browsing on sediment particles, which become too large to ingest (Lopez and Levinton, 1978; Lopez and Kofoed, 1980; Taghon, 1982). The response of covering rates as regards microphytobenthic biomass thus seems to be totally different when snails crawl either on silt-clay or on sand particles. Both microphytobenthic biomass and particle size are relevant factors that have to be investigated simultaneously to quantify their single and interactive influences on their feeding and crawling activities.

Forbes and Lopez (1986) also observed that snails aggregated in chl a enriched patches, where a decrease in covering rates occurred, while feeding rates remained constant. They concluded a snail attraction to diatom patches. We could also have expected such a patch selection to occur in our experiments. However, we observed that more snails crawled onto chl *a* enriched sediments than non-enriched sediments (Figs. 4 and 5) just in one special case (i.e. lit-conditions and in absence of water). This difference was not significant and all other experiments showed that more snails crawled on non-enriched sediments than on

503 enriched sediments. Forbes and Lopez (1986) concluded a patch–selection exerted by
504 Hydrobia species, but this might not take place as an attraction to diatom patches, but rather as
505 a direct consequence to a decrease in crawling activities that they observed in patches where
506 chl a concentrations were very high (108 $\mu g.g^{-1}$). Assuming that snails slow down in a given
507 area where snail displacements are realised randomly, they will have a natural tendency to
508 aggregate in this given area. Such a hypothesis can be confirmed by using a random-walk
509 model as those developed by Mac Nally (2000) or Blanchard et al. (2000) by considering a
510 decrease in snail mobility in a local area. As we did not observe such a decrease in covering
511 rates induced by increase in chl a concentrations for our experimental conditions, it was thus
512 not surprising that we observed no significant tendencies of snails to aggregate on sediment
513 enriched in chl *a*.
514
515 4.4 Interacted effects of light and microphytobenthic biomass

516 Differences in covering rates between enriched and non-enriched sediment were more
517 significant for experiments performed with light than without light (Fig. 7) and especially
518 without seawater covering. We can suggest that diatom influence is much exerted in
519 environmental conditions that permit microphytobenthos migration and biofilm constitution
520 i.e. exposed to light and without seawater. Indeed, many deposit-feeders, and especially
521 surface deposit-feeders, feed from a discrete zone of the sediments. In these instances,
522 analysis of a big volume of total mud mixture as an indication of available food particles
523 would be erroneous, because microphytobenthic cells have an endogenous rhythm, based on
524 synchronisation with diurnal periods of emersion, which make them migrate towards sediment
525 surfaces, where they accumulate (Serôdio et al., 1997; de Brouwer and Stal, 2001). When a
526 sediment is taken from an intertidal mudflat, diatoms which live in this sediment, can express
527 their endogenous rhythm after removal of environmental stimuli for ca. 3 days with a

528 migratory response decreasing in magnitude (Serodio et al., 1997). The simulating of an
529 experimental tidal cycle in presence of light, that mimics *In situ* tidal cycle, allows diatom
530 migratory rhythm to keep its magnitude and to be prolonged for more than one week
531 (Blanchard et al., 2001). So, we suggest that our experimental conditions allowed diatom
532 patches to appear at air/sediment interface when the sediment was illuminated without
533 seawater rather than for other tested conditions. Without light, diatom positive influence also
534 occurred because chl *a* concentration of the sediment mixture was 15 $\mu g.g^{-1}$, compared to a
535 non-enriched sediment with a chl *a* concentration equal to 1 $\mu g.g^{-1}$. However, when snails and
536 sediment were exposed to light, chl *a* concentrations at sediment surface were likely to be
537 more than 15 $\mu g.g^{-1}$ and diatom influences were likely to be exacerbated. Diatom
538 concentrations and light are thus 2 factors which are positively interrelated and they increase
539 snail crawling activities.

540 Since the experimental period lasted 24 hours with numerous observations, we can
541 focus on response linearity of covering rates versus activity time to test hypotheses about snail
542 endogenous rhythm, which were formulated by Newell (1962). Several experiments provided
543 suitable kinetics to detail snail activities for the 24-hour total experimental period. Among our
544 experiments with 1,000 $snails.m^{-2}$ (i.e. Figs. 2j, 2k, 2l, 3d, 3f, 3e and 3j) and with 5,000
545 $snails.m^{-2}$ (i.e. 3e, 3f, 3j), we observed an increase in snail activity after 5 hours and neither
546 Von Bertalanffy nor logistic models could provide reliable simulation of this pattern (Figs. 2
547 and 3). All experimental conditions were constant during the total experimental period and
548 this could have suggested that snails exhibited an endogenous rhythm, making their covering
549 rates suddenly increase after 5 hours. However, our experiments, where such an increase in
550 activity occurred, were always experiments performed with chl *a* enriched sediment, and we
551 thus suggest that this increase in snail activity was directly related to the presence of diatoms.
552 The occurrence of diatom migratory processes can be evoked once again to explain our

553 results, because the *In situ* diurnal low tide occurred 5 hours after the beginning of our
554 experiments, when the increase in snail activity took place. The fact that more snails crawled
555 after 5 hours provides an alternative explanation to the increase in covering rates. However,
556 we have rejected this alternative hypothesis because the increase in covering rates was
557 observed only for sediments enriched in chl *a* (Figs. 2 and 3), whereas changes in behaviour
558 occurred in all experiments (Figs. 4 and 5). Moreover, including crawling snail densities
559 instead of total snail densities in Von Bertalanffy models (Eq. 5) did not guarantee better fits
560 to crawling kinetics. These increases in crawling activities are thus further evidence of the
561 positive influence of diatoms and of their migratory processes for controlling snail crawling
562 activities. Our interpretations allow us to explain the increase in snail activities without
563 disagreeing with studies that demonstrated that no endogenous rhythm exists for Hydrobia
564 species (Little and Nix, 1976; Barnes, 1981a; 1981b and 1986).

565 Newell (1962) found a direct effect of luminosity on floating snail densities after 15
566 minutes. We found similar results for all sediment moisture content, when the sediment was
567 enriched in chl *a*, but opposite results when sediment was not enriched in chl *a*. In light of this
568 additional information, we still insist on the interaction of both microphytobenthic biomass
569 and light to affect snail activity levels.

570

571 4.5 Effects of light

572 Our interpretations, which are based on the positive interrelated influences of light and
573 microphytobenthic biomass, do not mean that light influences on covering rates are totally
574 mediated throughout microphytobenthos influences, because light influences were also
575 exhibited for sediment non-enriched in chl *a*. Apart from one experiment, where snails were
576 covered by water and sediment was enriched in chl *a*, all our experiments showed that more

577 snails were active in the light than in the dark (Comparison between Figs. 7 and 8). Barnes
578 (1986) used undisturbed samples to test different combinations of the presence and absence of
579 light and of cover by seawater and we found contradictory results to his, since he concluded:
580 “greater proportion of snails were active in the dark than in the light”. E may suggest that, in
581 his experiments, Barnes might have confused light intensity effects with temperature effects
582 because his core samples exposed to light were subject to *In situ* temperature fluctuations at
583 the same time as luminosity fluctuations. He observed similar fluctuations when sediment was
584 submerged but, to a lesser extent, than when compared to low-tide damp conditions. In these
585 submerged conditions, temperature effects could be amortised, but still occurred to affect their
586 results. Throughout the whole process of our experiments, the temperature was maintained at
587 17°C to ensure that this factor would not affect our results.
588
589 4.6 Behavioural processes

590 We also showed that no model improvement can be guaranteed by considering
591 behavioural processes because time-scale involved in crawling kinetics were low (Figs. 2 and
592 3) compared to time-scale involved in behavioural changes (Figs. 7 and 8). Indeed, most of
593 the inactive snails reacted very rapidly (sometimes within 1 minute) before crawling, whereas
594 increase in crawling rates often appeared after 5 hours. Consequently, variations in crawling
595 snail density are not a relevant factor to explain variations in crawling kinetics.

596 On the other hand, Levinton (1979) reported that floating population never exceeded
597 more than one per cent of those on the sediment of *In situ* conditions and we suggest that
598 floating behaviour does not occur similarly between microcosms and *In situ* because, in the
599 latter conditions, “snails do emigrate throughout floating when the tide rises or falls”.
600 Similarly, Armonies and Hartke (1995) estimated that only 1 percent of snails float per day.
601 We conclude that environmental factor influences play an important role in crawling and

feeding activities, but that no direct application can be extracted from floating behaviour results. Only crawling activities are relevant criteria for our purposes.

5. Conclusion

Compared to active or floating snail proportions, crawling kinetics have the advantage to integrate simultaneously individual and population components on activity levels, as they depend on individual covering rates and on crawling snail densities. Analysis of crawling kinetics and covering rates leads us to conclude the positive influence of sediment moisture content, water cover and light on snail activity levels. Snail mobility increases the probability of encountering the side walls of microcosms with subsequent upward movements and floating and this behaviour thus appears to be an experimental bias due to microcosm confinement. We finally conclude that microcosm floating snail proportions are not a reliable criterion to describe snail activity variations compared to covering rates and these proportions can simply qualitatively confirm previous results obtained from covering rate analysis.

We are in agreement with Barnes (1986) when he says that Hydrobia species react to changes in ambient environmental conditions, but contrary to his results, our covering rate analysis reveals an exciting single effect of light, which could be positively interrelated to a diatom effect. Above all, Hydrobia activities can only occur in the presence of seawater either by submersion, or by presence of fluid layers in low-tide conditions. We also suggest the relevance of diatom biomass as an interrelated-light variable and suggest that recent findings on microphytobenthos processes (Serôdio et al., 1997; Guarini et al., 2000; Blanchard et al., 2001; de Brouwer and Stal, 2001) have to be further investigated to revisit Hydrobia ulvae activities.

This study reveals the complex interrelationships between all investigated variables and we recommend caution to consider single effects of one environmental abiotic variable,

627 which can be correlated with other confusing variables. Effects of abiotic environmental
628 factors on foraging behaviour must be studied as a whole in evaluating the optimality of
629 foraging behaviour and factors as particle size, diatom biomass, sediment moisture content,
630 cover by seawater, light regime and temperature are all likely to affect snail activity and must
631 be crossed factors into drastic experimental designs to propose a realistic general overview of
632 crawling/feeding activities of intertidal mudflats.

633 The proposed model based on Von Bertalanffy equations includes 10 parameters to
634 describe kinetics of sediment covering by snail tracks under the influence of snail density,
635 sediment moisture content, chl *a* concentrations and the four combinations of
636 presence/absence of light and seawater. The diatom biomass effect should be further
637 reviewed because only 2 chl a concentrations were tested for minimisation tests within a very
638 small range. Furthermore, comparison with other studies (Forbes and Lopez, 1986) suggests
639 to us that Eq. 15 is not reliable for the very high chl *a* concentrations. For further
640 development, our model will also have to be validated by direct confrontation with *In situ*
641 crawling results reported for wild animals. This would imply some corrections because
642 moderate or severe artefacts may arise from using enclosures that are too small, which could
643 produce inferential nonsense in some circumstances (Mac Nally, 2000).

644 Finally, since Hydrobia bioturbation activities are dependent on environmental factors
645 throughout track formation processes, this model should provide a base for further
646 hydrosedimentary development to simulate the effects of H. ulvae bioturbation activities on
647 the resuspension of the intertidal cohesive sediment-water interface in various *In situ*
648 conditions.

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Table 1. Notation used in equations.

Variables and parameters	Definition and units	Equations
Variables		
S	Total microcosm surface (m^2)	1,3,6
T	Bioturbated surface (i.e. covered by Tracks) (m^2)	1,3,
ϕ	Bioturbated surface relative to total microcosm surface (%)	2,3,4,5,6,10,11
n	Snail density ($snail.m^{-2}$)	1,2,4,5,11,12
W	Sediment moisture content (%)	13,14,15
chl*a*	Sediment Chlorophyll a concentration ($\mu g.g^{-1}$)	15
t	Activity time (h)	1,2,4,5,6,7,8,9,10, 11,12
A	State behaviour matrix	7,9
I	Inactive snail density ($snail.m^{-2}$)	7,9
C	Crawling snail density ($snail.m^{-2}$)	7,9
B	Burying snail density ($snail.m^{-2}$)	7,9
F	Floating snail density ($snail.m^{-2}$)	7
Constant and parameters		
P	Probability that a snail meets an old-formed track	1,2,3
a	Covering rate ($m^2.h^{-1}.snail^{-1}$) in the Von Bertalanffy model	1,2,4,5,14
a^P	Population covering rate ($m^2.h^{-1}$) in the Von Bertalanffy model	6
α	Covering rate ($m^2.h^{-1}.snail^{-1}$) in the logistic model	11
α	Population covering rate ($m^2.h^{-1}$) in the logistic model	10
t_{50}	Constant of integration relative to the covering rate in the logistic model (h)	11
t^P_{50}	Constant of integration relative to the population covering rate in the logistic model (h)	10
Ω	Transition behaviour matrix	7,9
T_{ij}	Probability that a snail that occupied a behaviour pool (i) occupy another behaviour pool (j) during a time interval (h^{-1}). i and j can be all 4 behavioural modes	7,8,9
k_{FI}	Maximal t_{FI} probability (h^{-1})	8
a_{FI}	Rate of increase of t_{FI} (h^{-1})	8
t^{50}_{FI}	Constant of integration relative to t_{FI} (h)	8
a_0	Covering rate when $W \rightarrow \infty$ and chl*a*=0 $\mu g.g^{-1}$ ($m^2.h^{-1}.snail^{-1}$)	12,13
f(W)	Moisture content dependence compound equation included in the Von Bertalanffy model	12,13,14
g(chl*a*)	Chl*a* content dependence compound equation included in the Von Bertalanffy model	12,13
W_{50}	Sediment moisture content dependent parameter in the Von Bertalanffy model (%)	14
η	Rate of increase of covering rate in function of W(no unit)	14
λ	Sediment moisture content dependent rate of increase in function of chl*a* (no unit)	15

Table 2. Covering rate estimates provided by Von Bertalanffy models including total snail densities and crawling snail densities.

Environmental conditions				Covering rates ($m^2.h^{-1}.snail^{-1}$)	
Day/Night	Low/High tide	[Chl a] in $\mu g.g^{-1}$	W %	Without behaviour	With behaviour
Light	Without seawater	1	106	0	0
			225	0	0
			382	$1{,}18.10^{-5}\pm6{,}56.10^{-6}$	$3{,}89.10\text{-}^{5}\pm7{,}61.10\text{-}^{6}$
		15	106	$2{,}60.10\text{-}^{5}\pm3{,}53.10\text{-}^{6}$	$8{,}29.10\text{-}^{5}\pm4{,}91.10\text{-}^{6}$
			225	$2{,}54.10\text{-}^{5}\pm1{,}00.10\text{-}^{5}$	$8{,}81.10\text{-}^{5}\pm1{,}25.10\text{-}^{5}$
			382	$1{,}09.10\text{-}^{4}\pm2{,}20.10\text{-}^{5}$	$3{,}25.10\text{-}^{4}\pm1{,}86.10\text{-}^{5}$
	With seawater	1	106	$2{,}62.10\text{-}^{6}\pm1{,}44.10\text{-}^{6}$	$8{,}49.10\text{-}^{6}\pm2{,}78.10\text{-}^{6}$
			225	$2{,}67.10\text{-}^{5}\pm1{,}51.10\text{-}^{6}$	$8{,}73.10\text{-}^{5}\pm2{,}85.10\text{-}^{5}$
			382	$8{,}35.10\text{-}^{5}\pm7{,}08.10\text{-}^{5}$	$2{,}68.10\text{-}^{4}\pm1{,}67.10\text{-}^{5}$
		15	106	$1{,}67.10\text{-}^{4}\pm3{,}64.10\text{-}^{5}$	$5{,}50.10\text{-}^{4}\pm3{,}36.10\text{-}^{6}$
			225	$1{,}26.10\text{-}^{4}\pm7\ ,72.10\text{-}^{5}$	$4{,}39.10\text{-}^{4}\pm5{,}60.10\text{-}^{6}$
			382	$1{,}96.10\text{-}^{4}\pm2{,}26.10\text{-}^{5}$	$6{,}67.10\text{-}^{4}\pm3{,}00.10\text{-}^{6}$
Darkness	Without seawater	1	106	0	0
			225	$1{,}04.10\text{-}^{5}\pm5{,}75.10\text{-}^{6}$	$6{,}15.10\text{-}^{5}\pm1{,}35.10\text{-}^{5}$
			382	$5{,}80.10\text{-}^{6}\pm7{,}33.10\text{-}^{6}$	$1{,}67.10\text{-}^{5}\pm7{,}59.10\text{-}^{6}$
		15	106	$8{,}09.10\text{-}^{6}\pm7{,}73.10\text{-}^{6}$	$2{,}32.10\text{-}^{5}\pm7{,}92.10\text{-}^{6}$
			225	$1{,}73.10\text{-}^{5}\pm3{,}91.10\text{-}^{6}$	$4{,}94.10\text{-}^{5}\pm4{,}04.10\text{-}^{6}$
			382	$1{,}26.10\text{-}^{5}\pm2{,}56.10\text{-}^{6}$	$3{,}49.10\text{-}^{5}\pm1{,}59.10\text{-}^{5}$
	With seawater	1	106	$1{,}18.10\text{-}^{6}\pm2{,}90.10\text{-}^{7}$	0
			225	$5{,}79.10\text{-}^{5}\pm1{,}71.10\text{-}^{5}$	$2{,}29.10\text{-}^{4}\pm2{,}75.10\text{-}^{6}$
			382	$7{,}61.10\text{-}^{5}\pm3{,}08.10\text{-}^{5}$	$2{,}42.10\text{-}^{4}\pm4{,}19.10\text{-}^{5}$
		15	106	$1{,}25.10\text{-}^{4}\pm1{,}92.10\text{-}^{5}$	$4{,}84.10\text{-}^{4}\pm9{,}33.10\text{-}^{7}$
			225	$6{,}79.10\text{-}^{5}\pm3{,}06.10\text{-}^{5}$	$2{,}14.10\text{-}^{4}\pm6{,}25.10\text{-}^{6}$
			382	$1{,}21.10\text{-}^{4}\pm1{,}88.10\text{-}^{5}$	$4{,}52.10\text{-}^{4}\pm1{,}76.10\text{-}^{6}$

Table 3. Estimates of final model parameters and their standard errors (Eqs. 12, 17 and 18).

	a_0 ($m^2.h^{-1}.snail^{-1}$)	W_{50} (%)	λ (no unit)	η (no unit)
In absence of seawater and light	$2{,}7.10^{-6}\pm0{,}1.10^{-6}$	160,3±1.6		
In presence of seawater and in absence of light	$26{,}6.10^{-6}\pm1{,}3.10^{-6}$	179,3±1,6	$44{,}3.10^{-3}\pm1.10^{-3}$	51,8±0.8
In absence of seawater and in presence of light	$15{,}8.10^{-6}\pm0{,}6.10^{-6}$	250,0±1.6		
In presence of seawater and light	$42{,}2.10^{-6}\pm3{,}1.10^{-6}$	199,8±4.4		

Figure captions

Fig. 1. Observation scale of tracks covering sediment surface: The real proportions of browsing areas were calculated using IMAGE-IN software.

Fig. 2. Time series of bioturbated areas in microcosms (* , o and + for 1,000; 5,000 and 10,000 snails.m^{-2}, respectively) compared to computed results (dashed, full and dotted lines for 1,000, 5,000 and 10,000 snails.m^{-2}, respectively) from Von Bertalanffy crawling models fitted to lit-condition experimental results.

Fig. 3. Time series of bioturbated areas in microcosms (* , o and + for 1,000; 5,000 and 10,000 snails.m^{-2}, respectively) compared to computed results (dashed, full and dotted lines for 1,000, 5,000 and 10,000 snails.m^{-2}, respectively) from Von Bertalanffy crawling models fitted to dark-condition experimental results.

Fig. 4. Time series of bioturbated areas in microcosms (o) compared to Lôpez-Figueroa and Niell (1987) results(×) in one experiment (10,000 snails.m^{-2} – W=106 % - [chl a]=15 µg.g^{-1} – light –seawater cover). Bioturbated areas simulated by using Von Bertalanffy model (full line) were calculated by fitting to both data sets.

Fig. 5. Relationship between covering rate estimates from Von Bertalanffy equations (Eq. 5) versus sediment moisture contents and chl a concentrations.

Fig. 6. Covering rates simulated by using Eqs. 12, 14 and 15 versus sediment moisture contents and chl a concentrations.

Fig. 7. Times series of proportion of snails that were crawling, floating, sinking and burying (+ , o , * and□ , respectively) in microcosms exposed to light compared to computed results from behaviour model (full, dotted, dashed and dashed-dotted lines, respectively).

Fig. 8. Times series of proportion of snails that were crawling, floating, sinking and burying (+ , o , * and□ , respectively) in microcosms exposed to darkness, compared to computed results from the behaviour model (full, dotted, dashed and dashed-dotted lines, respectively).

Figure 1

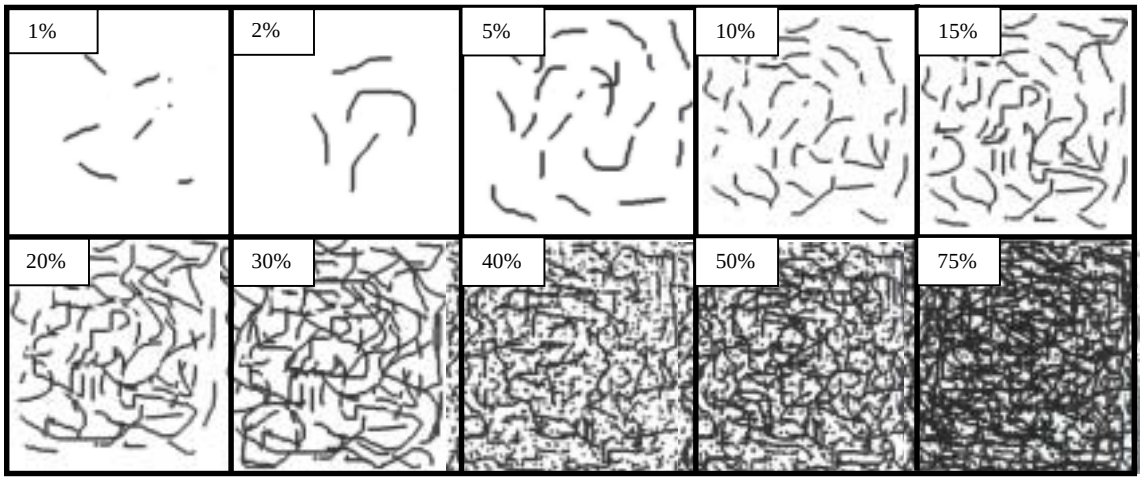


Figure 2

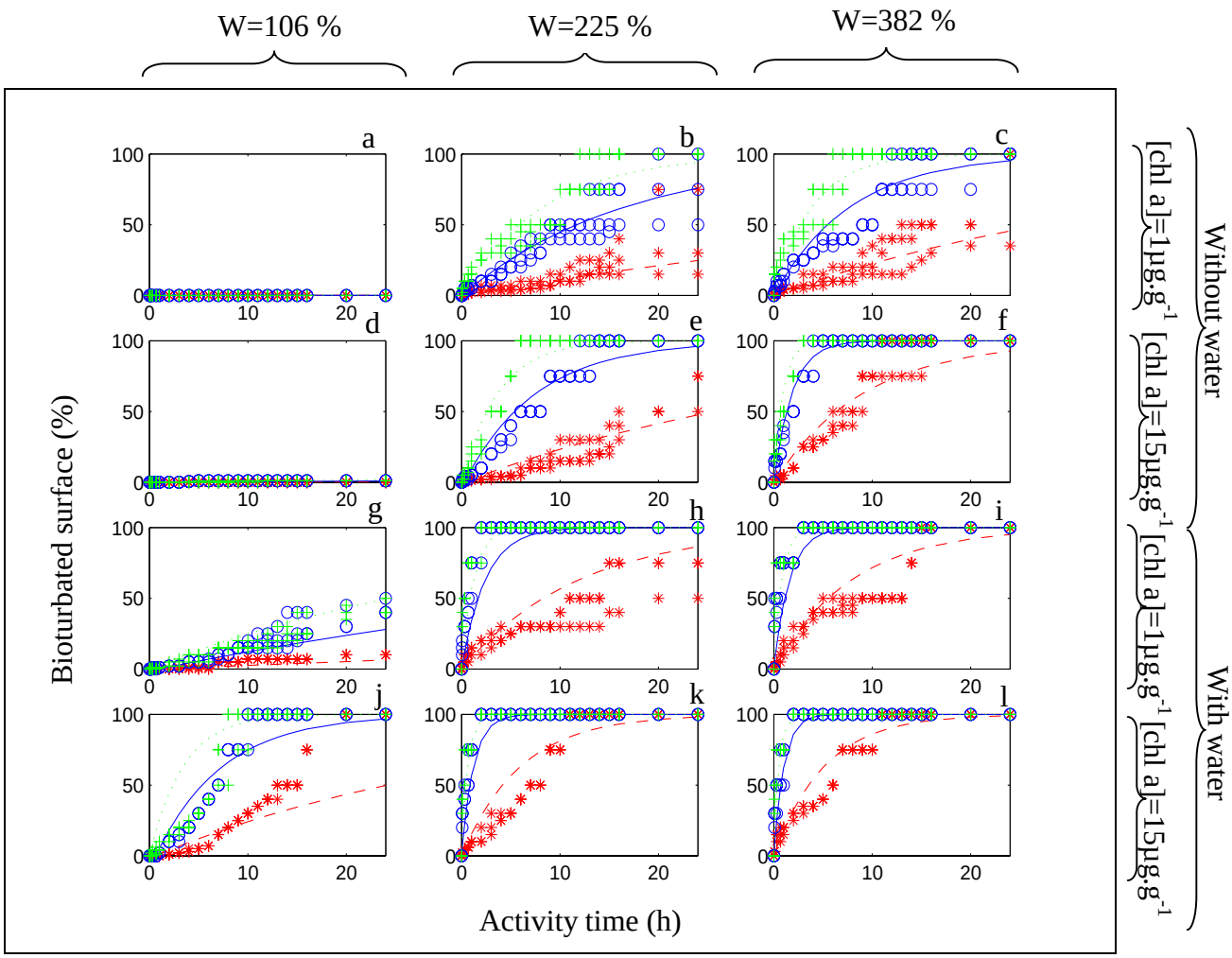

W=106 %
W=225 %
W=382 %
Bioturbated surface (%)
Activity time (h)
a
b
c
d
e
f
g
h
i
j
k
l
Without water
With water
[chl a]=1µg.g-1
[chl a]=15µg.g-1
[chl a]=1µg.g-1
[chl a]=15µg.g-1

Figure 3

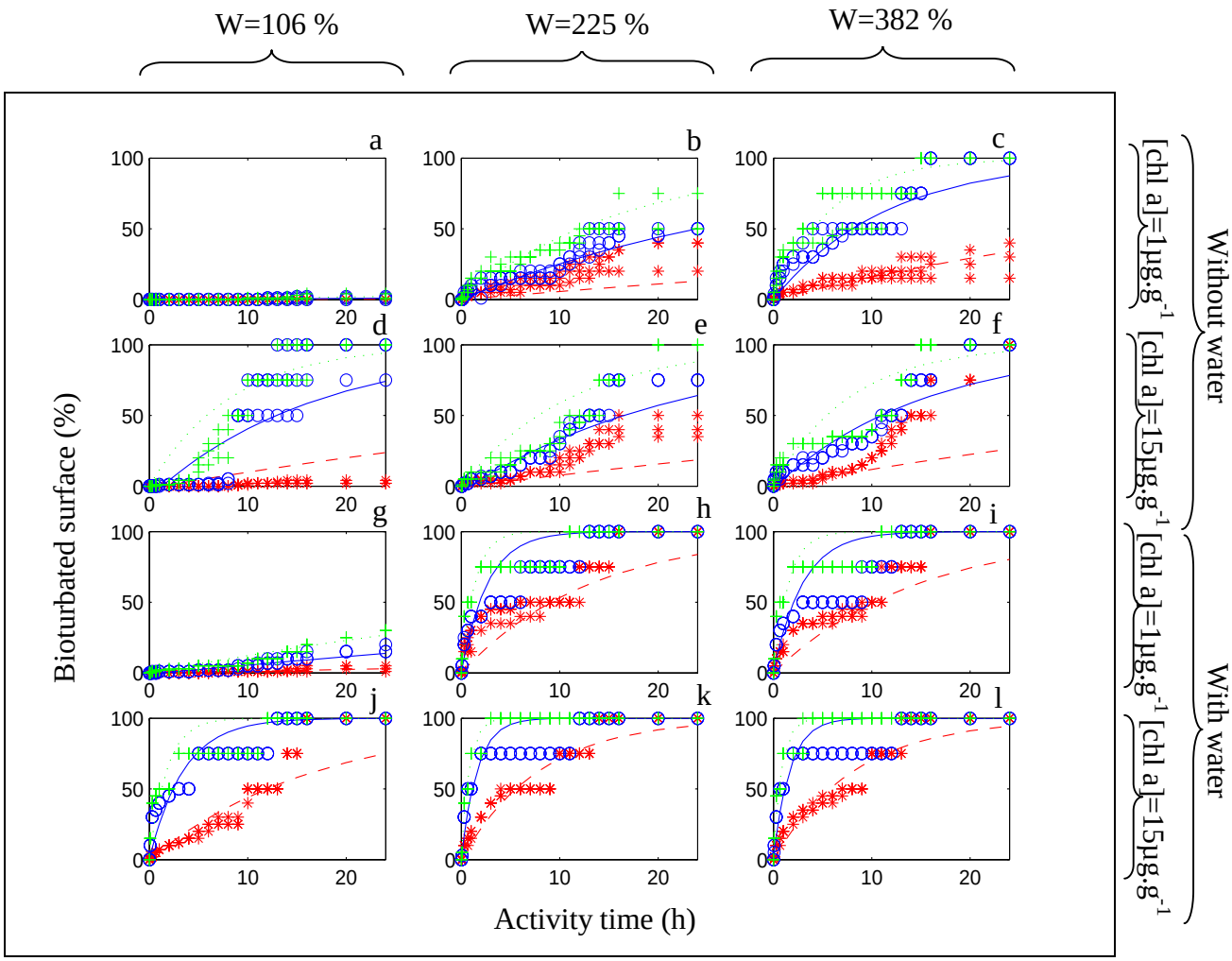

W=106 %
W=225 %
W=382 %
Without water
With water
[chl a]=1µg.g-1
[chl a]=15µg.g-1
[chl a]=1µg.g-1
[chl a]=15µg.g-1
Bioturbated surface (%)
Activity time (h)
a
b
c
d
e
f
g
h
i
j
k
l

Figure 4

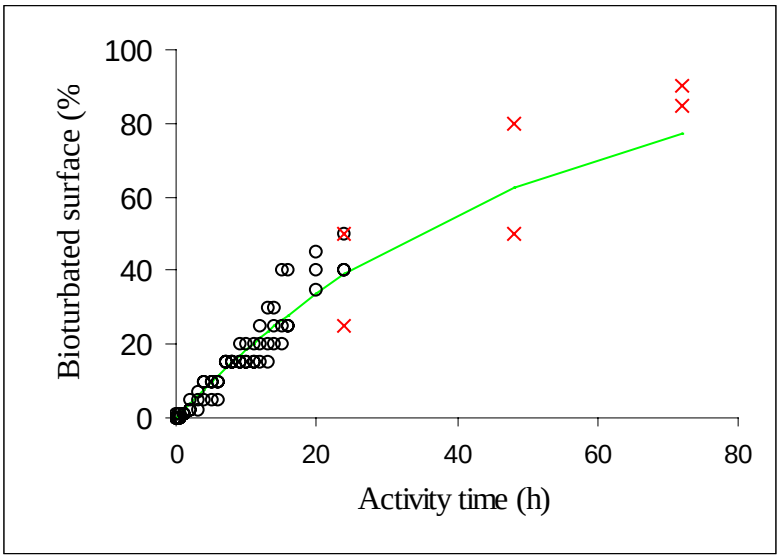

Bioturbated surface (%
100
80
60
40
20
0
0
20
40
60
80
Activity time (h)

Figure 5

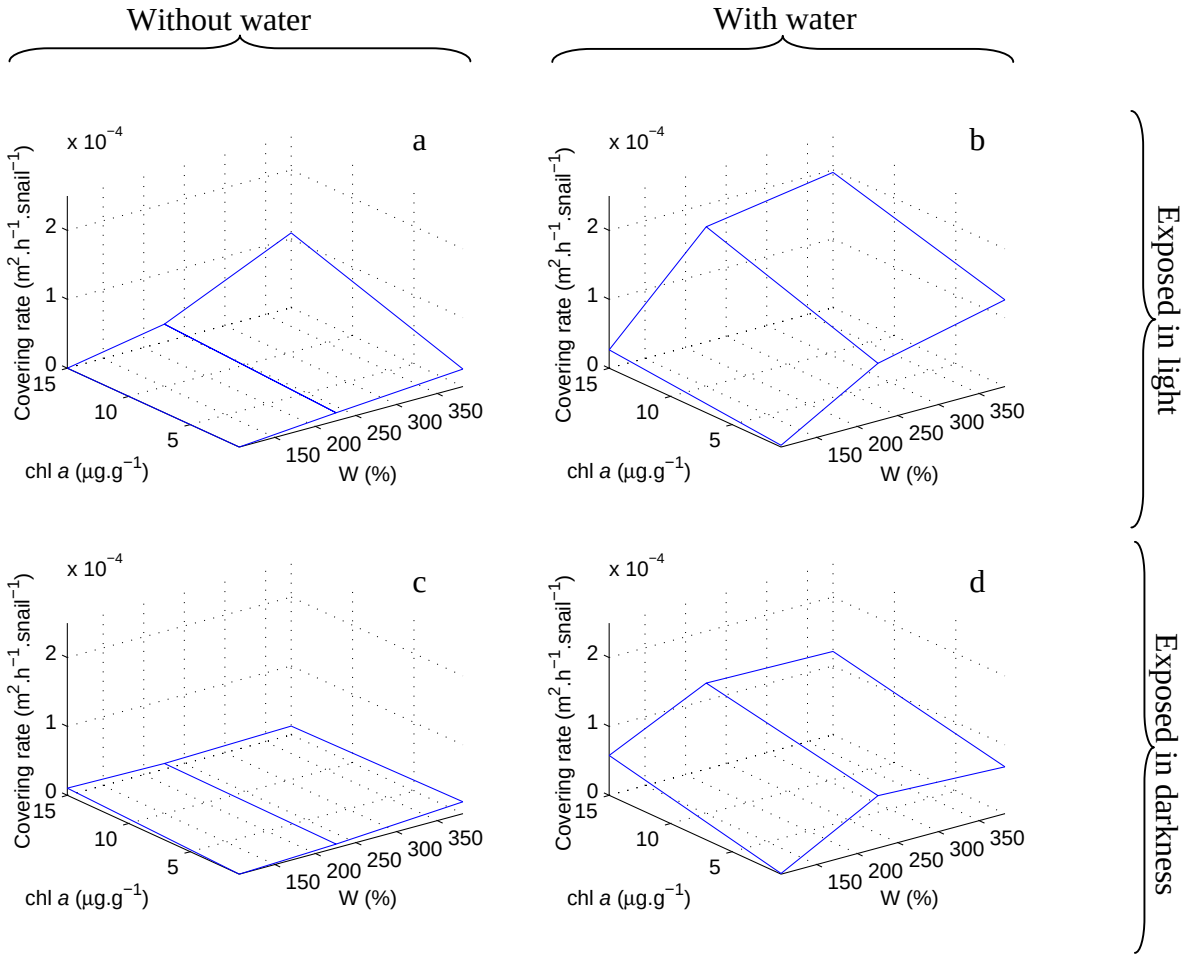

Without water
With water
Exposed in light
Exposed in darkness
a
b
c
d
x 10^{-4}
Covering rate (m^2.h^{-1}.snail^{-1})
chl *a* (µg.g^{-1})
W (%)
0
1
2
15
10
5
150
200
250
300
350

Figure 6

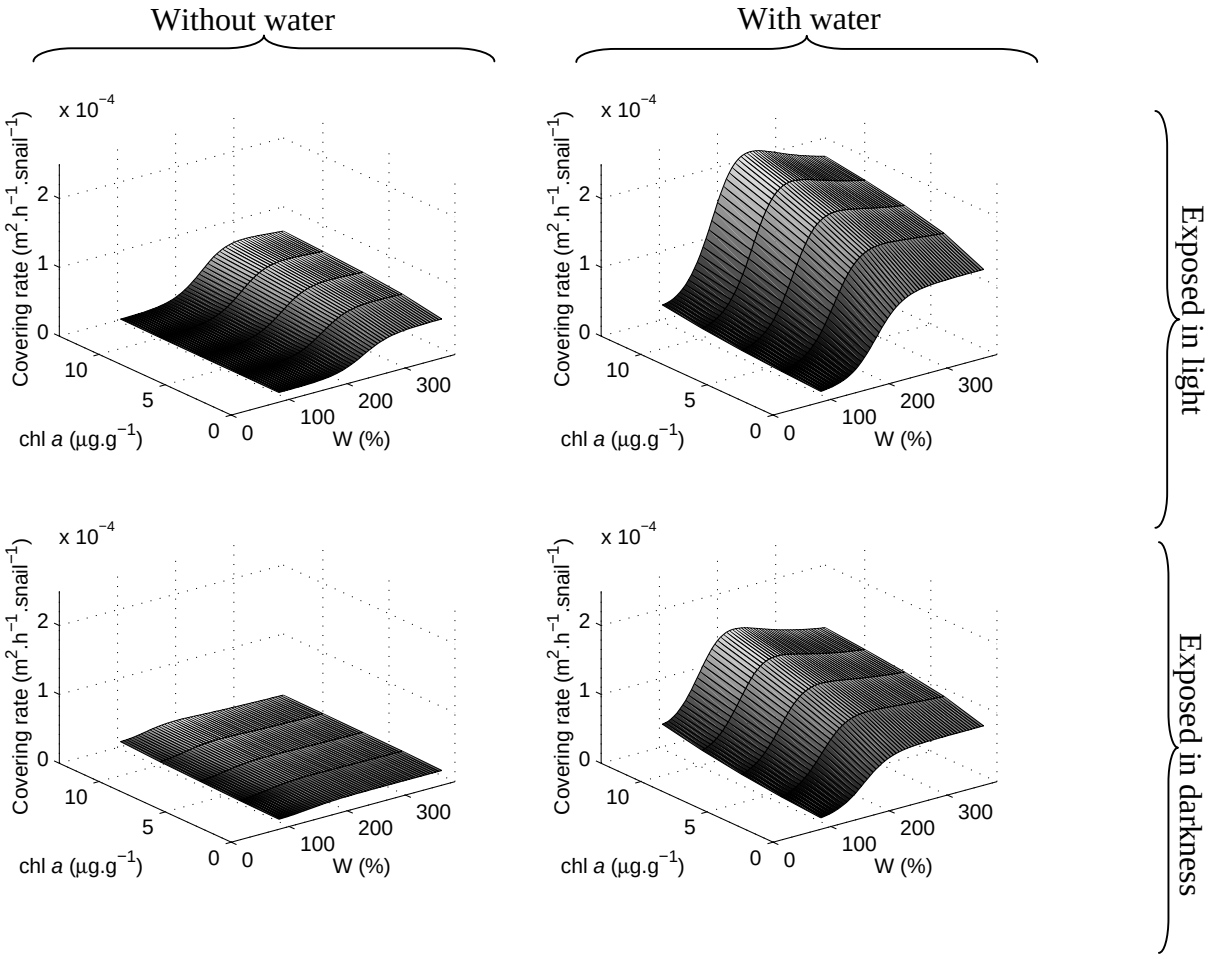

Without water
With water
Exposed in light
Exposed in darkness
x 10^{-4}
Covering rate (m^2.h^{-1}.snail^{-1})
chl *a* (µg.g^{-1})
W (%)
0
1
2
10
5
100
200
300

Figure 7

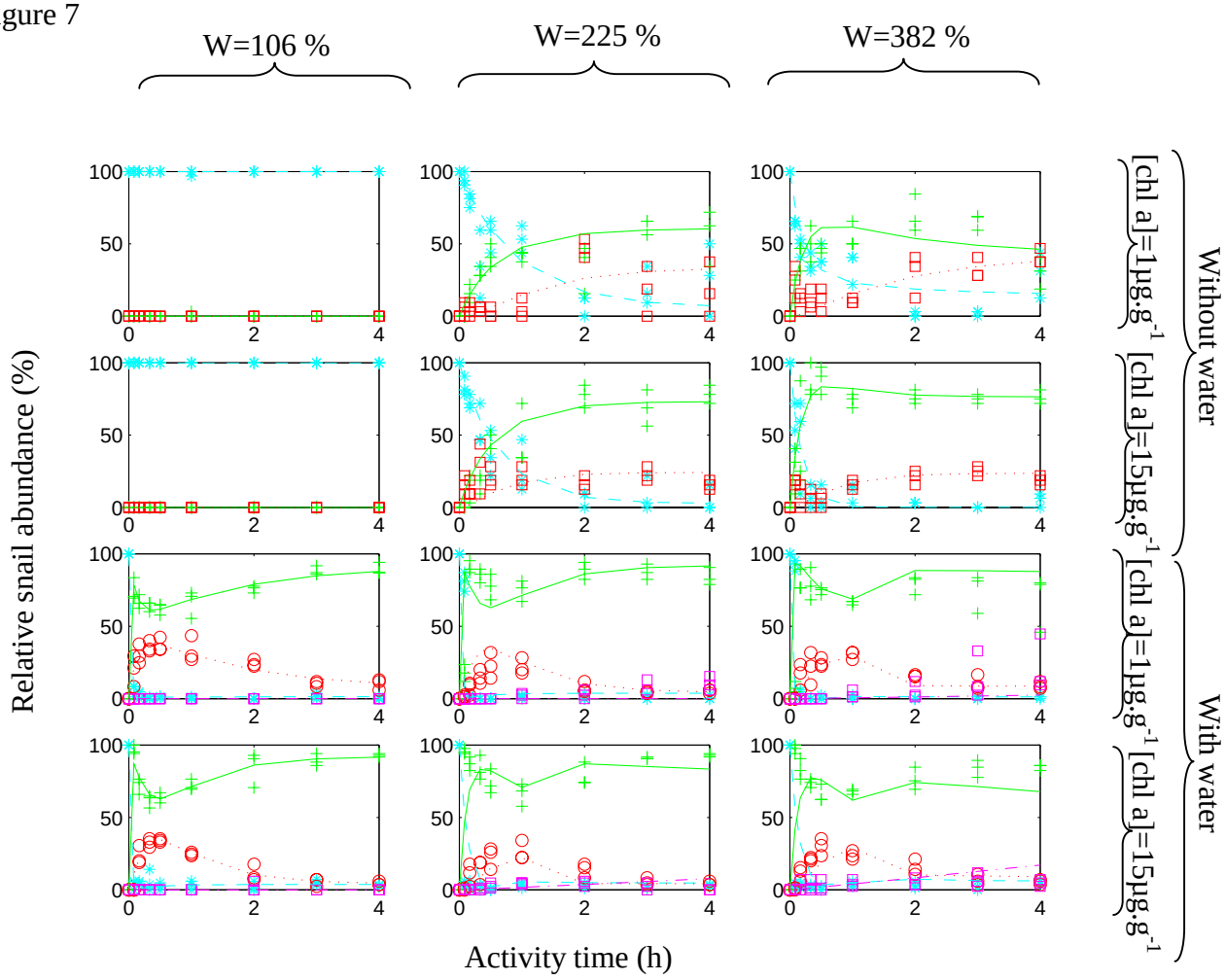
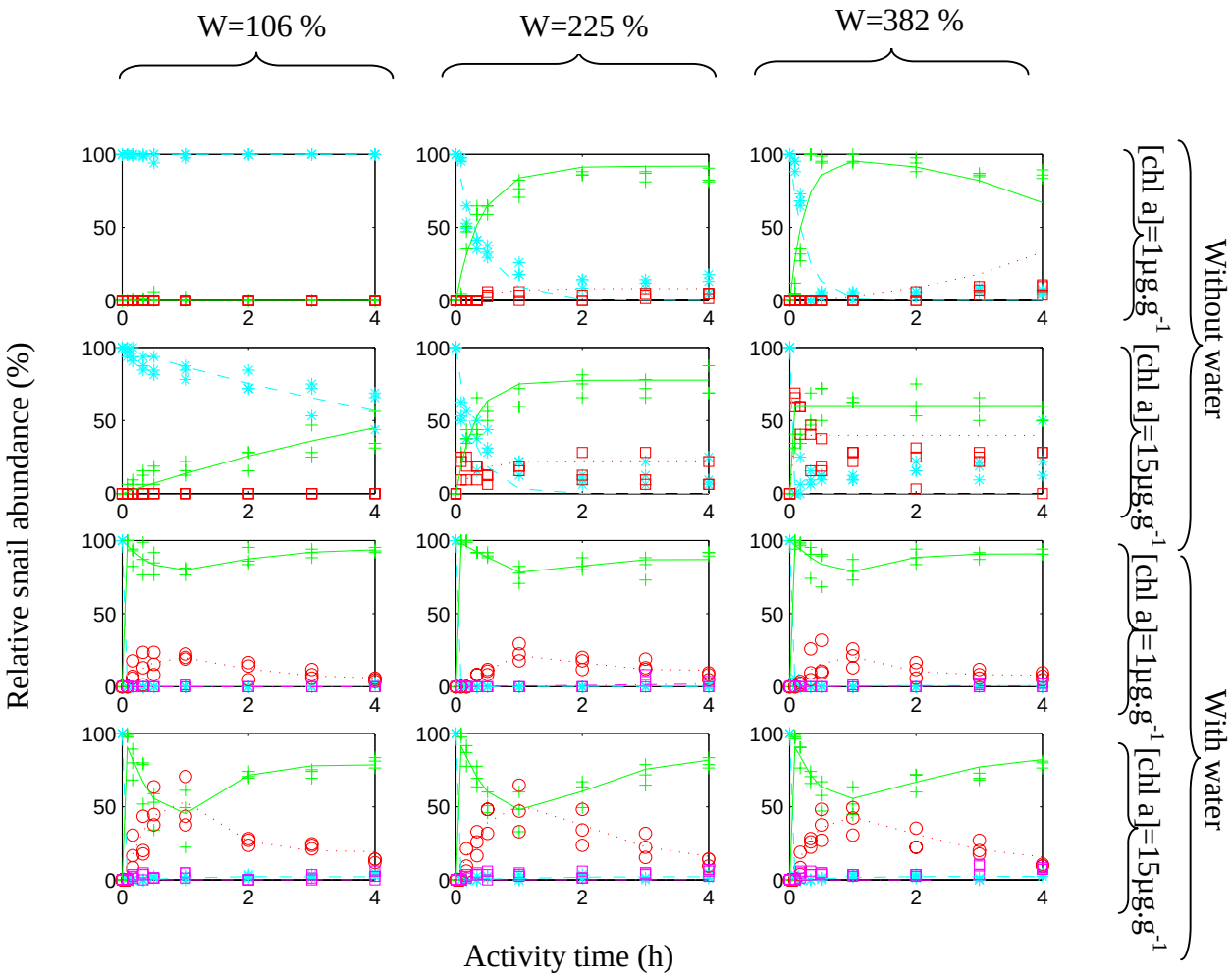

W=106 %
W=225 %
W=382 %
Relative snail abundance (%)
Activity time (h)
Without water
With water
[chl a]=1µg.g-1
[chl a]=15µg.g-1
[chl a]=1µg.g-1
[chl a]=15µg.g-1

Figure 8


W=106 %
W=225 %
W=382 %
Relative snail abundance (%)
Activity time (h)
Without water
With water
[chl a]=1µg.g-1
[chl a]=15µg.g-1
[chl a]=1µg.g-1
[chl a]=15µg.g-1