

# Linking predator kairomones and turbulence: synergistic effects and ultimate reasons for phenotypic plasticity in *Daphnia cucullata*

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With 4 figures

**Abstract:** The seasonal change in helmet size in *Daphnia cucullata* has been studied for over one century. Recently it has been shown that helmets in *D. cucullata*, which have been found to reduce predator caused mortality, can be induced by chemical cues released by several predatory invertebrates. However, it also has been shown that turbulence induces this trait. The relation and interplay of both inducing cues is not known. Here we present results from lab experiments showing that predator cues and turbulence can act synergistically. Both factors in combination induced significantly larger responses, compared to each factor alone, and helmets reached the maximum sizes found in natural lakes. This result might help to explain the observation of large helmets in this species in nature. The ultimate reason behind the turbulence induction is yet unknown. We link both induction factors to predation, as the ultimate reason, by testing the hypothesis that *D. cucullata* can respond to turbulence produced by swimming invertebrates. We found that helmet growth increased significantly in direct contact to both the heterospecific *Daphnia magna* and the predator *Cyclops* sp. Treatments which accounted for chemical cues alone did not increase helmet growth in response to cues from *D. magna*, or *Cyclops* under these conditions. Together, these results indicate that *D. cucullata* is able to respond to mechanical cues produced by swimming invertebrates. Thus, our study suggests that both chemical cues and turbulence generated by predatory invertebrates might act synergistically to induce helmets as effective protection against invertebrate predation.

**Key words:** cyclomorphosis, random flow, inducible defence, helmet, synergistic effects.

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## Introduction

In several *Daphnia* species, individuals present in early summer start to produce a long pointed helmet, which reaches its peak expression in the summer populations and gradually decreases again, until the winter and spring animals show a typical round head again (JACOBS 1987). *Daphnia cucullata* is a prominent example for the study of cyclomorphosis (LAMPERT & WOLF 1986). This seasonal change in morphology in *D. cucullata* has been experimentally studied for over 100 years (OSTWALD 1904). In the beginning, this morphological adaptation was assumed to aid *D. cucullata* to survive in the face of variation in the physical environment (WESENBERG-LUND 1900). Abiotic factors such as temperature (OSTWALD 1904) were regarded as inducing cues. Recently, the focus on the role of these morphological traits has changed, and defensive mechanisms they might provide have gained the explanatory role. Spines and helmets in cladocerans have been regarded as defences against predatory invertebrates (DODSON 1974) and both the induction and defensive effect have been demonstrated in a number of species (e. g., GRANT & BAYLY 1981, KRUEGER & DODSON 1981, HEBERT & GREWE 1985, DODSON 1989, HANAZATO 1991, TOLLRIAN 1994, KRIZAN-LÜNING 1997, reviewed in TOLLRIAN & DODSON 1999, LASS & SPAAK 2003). TOLLRIAN (1990) showed that also in *D. cucullata* helmets can be induced with chemical cues (kairomones) released by predacious *Chaoborus*-larvae and LAFORSCH & TOLLRIAN (2004a) showed that the helmets act as a multi-tool against a range of predatory invertebrates during different ontogenetic stages and via different mechanisms. Helmets benefit small *D. cucullata* early in their development against small predators e. g., copepods, and in later instars against larger invertebrate predators such as *Leptodora kindtii* and *Chaoborus*-larvae.

Despite the clear benefit imparted by induced helmets in lowering predation mortality, LAFORSCH & TOLLRIAN (2004b) returned to BROOKS (1947) and HRBÁČEKS (1959) earlier studies on turbulence and found that even larger helmets can be induced with a special kind of small-scale random flow (in this paper called turbulence). However, the ultimate reason for the induction of helmets by turbulence remains elusive. One possible explanation might be that the induced traits provide hydrodynamic benefits in turbulent conditions. Nevertheless, this hypothesis seems questionable as the arguably greatest period of turbulence, which occurs in spring and autumn when the lakes are mixed by wind action, does not coincide with the large helmets in nature (LAFORSCH & TOLLRIAN 2004b). However, the ability to sense small-scale turbulence could possibly be a second sensory system to detect predators. Mechanoception is an important sensory system in aquatic environments (ATEMA et al. 1988) and planktonic organisms have been found to produce turbulence. For example, GRIES et al. (1999) were able to measure the 'footprints' of

*Daphnia* in water, and small-scale turbulence generated by the movement of aquatic animals has been reported to signal both the vicinity of predators and the trace of potential prey organisms (TITELMAN & KIORBOE 2003, BUSKEY et al. 2002, KIORBOE & VISSER 1999, VISSER 2001, JIANG & OSBORN 2004). Copepods, especially, can distinguish between predator and prey hydromechanically (HWANG & STRICKLER 2001), pelagic copepods use hydromechanical signals for mate recognition (KIORBOE & BAGOIEN 2005, BAGOIEN & KIORBOE 2005), and a study by BOLLENS & FROST (1989) even indicated that hydromechanical stimuli from fish induced diel vertical migration in marine copepods. Furthermore, chemoperception could be modulated by the surrounding flow field of a pelagic copepod (JIANG & OSBORN 2004).

The aims of our study were firstly to test possible synergistic effects of turbulence and predator cues on helmet formation in *Daphnia cucullata* and secondly, to test the hypothesis that both small-scale turbulence and predator-released chemicals can be linked to predation with a defensive effect as ultimate reason for helmet formation. We studied helmet formation in *D. cucullata* in response to turbulence, kairomones and a combination of both to test for synergistic effects. To link turbulence to predation, we tested whether turbulence created by swimming invertebrates can induce helmets. We compared helmet growth in three different set-ups: in direct contact with two invertebrates, the herbivore *Daphnia magna* or the predatory copepod *Cyclops* sp., in net cages which blocked the predators and their turbulence but allowed chemical cues to pass, and in control treatments without predators.

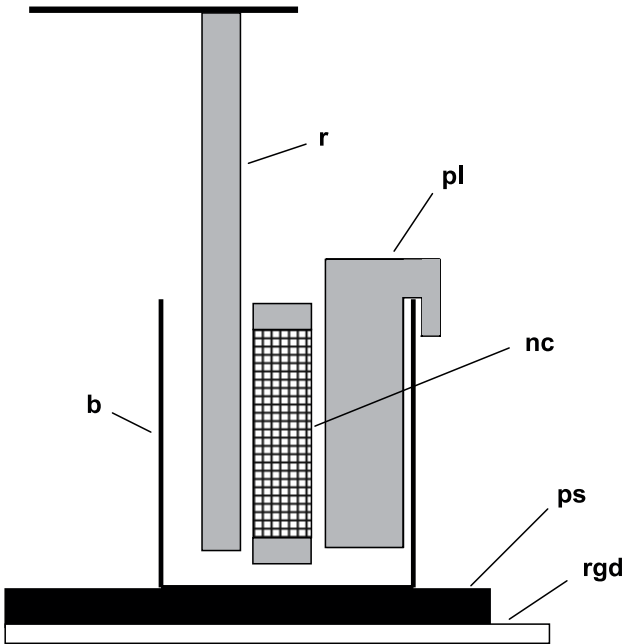
## Material and method

We used a single laboratory-cultured clone of *D. cucullata* for our experiments. This clonal line originated from Lake Thalersee (Germany) and has been proven to show distinct morphological responses to predators and turbulence (LAFORSCH & TOLLRIAN 2004a, b).

All experiments were conducted in artificial medium (JESCHKE & TOLLRIAN 2000) to exclude natural chemical signals, at  $20 \pm 1^\circ\text{C}$  in a temperature-controlled room under fluorescent light (16 h : 8 h day : night rhythm). The medium was changed weekly in each beaker. A pure culture of *Scenedesmus obliquus* was fed daily at a concentration of 1.5 mg C/L to the daphnids. Age-synchronized cohorts of *Daphnia* were grown prior to the experiments by collecting mothers with freshly deposited eggs. The third brood of these mothers was used for the experiments. All treatments were replicated three times (each beaker being a replicate) and lasted three weeks, to take possible transgenerational effects into account (AGRAWAL et al. 1999).

## Artificial turbulence and kairomones

When we use the term turbulence in this paper we actually mean a process defined in fluid dynamics as random flow (OSBORN 1996). The proof that random flow is turbulent is not easy and has not been made for our set-up. However, we use the term turbulence to be consistent with the ecological literature (BROOKS 1947, HRBÁČEK 1959). The same experimental design was used as described in detail in LAFORSCH & TOLLRIAN (2004 b). Here we used the design described as Turbulence-2-set-up. In brief, small-scale turbulence was generated in 1.5 L glass beakers by a permanently stirring rod (30 rpm), creating laminar flow, which was broken and transformed into turbulence by an acrylic plate attached to the wall of the beaker (Fig. 1). Cylindrical net-cages (4 cm diameter  $\times$  15 cm height), made of plankton netting gauze (100  $\mu\text{m}$  mesh-size) glued to small acrylic-tubes, were placed into the beaker. Ten fourth instar larvae of *Chaoborus flavicans*, isolated from Lake Klostersee were placed into the net-cages, to prevent direct predatory effects but to ensure the exchange of chemical cues. *Chaoborus* larvae were fed daily with 30 non-induced individuals of *D. cucullata*. The net-cages were cleaned and dead or pupate *Chaoborus* larvae were replaced everyday. Beakers containing net-cages without predators served as control. Both experiments were started by introducing 30 age-synchronized mothers of *D. cucullata* randomly into each beaker.



**Fig. 1.** Schematic line drawing of the Turbulence-2-set-up: Abbreviations: rgd = permanently rotating gel dyer; ps = polystyrene sheet; r = acrylic rod; pl = acrylic plate; b = beaker; nc = net-cage (modified figure from LAFORSCH & TOLLRIAN 2004 b).

### **Turbulence evoked by *Daphnia magna***

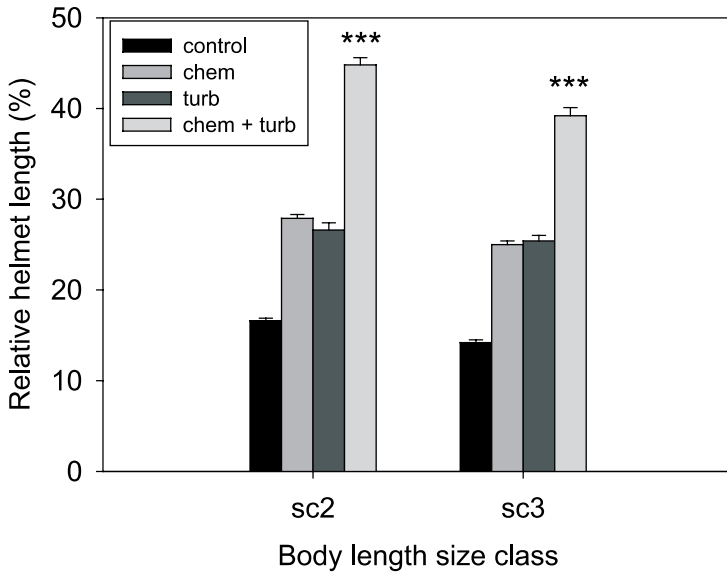
Laboratory cultured *D. magna* (originating from Ismaninger Speichersee, Germany) were selected to elucidate if the inducing small-scale turbulence is generated by the movements of invertebrate plankton organisms. Thirty age-synchronized adult individuals of *D. cucullata* and 15 *D. magna* were placed together into 1.5 L glass beakers. Each beaker contained a net cage as described above. The net cage allowed chemical cues to pass, but acted as a shield against small-scale turbulence. We had previously tested the shield effect in experiments with stained water. To control for the inducing effect of chemical compounds released by *D. magna*, additionally 12 adult *D. cucullata* were placed into each net-cage. The density of *D. magna* was reduced to 30 individuals, following reproduction, in a seven-day interval to avoid food limitation for *D. cucullata*. Beakers without *D. magna* served as control.

### **Kairomones and turbulence evoked by predatory invertebrates**

Cyclopoid copepods (body size  $1.8 \pm 0.2$  mm) were isolated from the Ismaninger Speicherseen, Germany. Two hundred *D. cucullata* were initially introduced into 1.5 L glass beakers to provide a sufficient amount of prey for the predators but to avoid the extinction of the population over the course of the induction experiments. Eight *Cyclops* sp. served as predators in the same beakers. We used the net-cages, as described above, to distinguish between helmet growth induced by predator-released chemicals (in the net-cages) and synergistic effects between those kairomones and turbulence (in direct contact). Twenty adult *D. cucullata* were placed into the net-cages at the beginning of the experiment. Beakers without *Cyclops* sp. served as control.

### **Data analysis**

After the experiments morphological parameters of the remaining *D. cucullata* from each beaker were recorded using a digital image-analysis system (Soft Imaging System, Analysis Pro, Münster, Germany). We measured the helmet length (defined as the length between the tip of the helmet to the upper edge of the compound eye), and the body length (defined as the length between the upper edge of the compound eye to the base of the tail spine). We included only animals of two size classes, with body length between 600–799  $\mu\text{m}$  (sc2, comprising instars 3 and 4) and 800–1000  $\mu\text{m}$  (sc3, comprising instars 5 and 6) in our analysis because our previous results had shown that morphological traits are most pronounced in this ontogenetic stage (LAFORSCH & TOLLRIAN 2004 a). These animals were a mix of F1, F2 and F3 offspring of the originally introduced mothers. The relative trait length (helmet length/body length \* 100) was calculated to compensate for size-dependent changes within each size class. These values were arcsin-square-root-transformed prior to analysis (SOKAL & ROHLF 1995). Data were tested for normal distribution and a nested ANOVA, with three replicates (beakers) per treatment as random factor, was calculated for the experiments to analyze for treatment effects between animals faced with environmental stressors and control daphnids. A Tamhane post-hoc test which is insensitive to unequal variances was used for pairwise comparisons. Statistics were calculated with SPSS V12.0 (SPSS Inc.).



**Fig. 2.** Synergistic effects between chemical cues released by *Chaoborus* (chem) and artificial generated turbulence (turb) regarding helmet induction in *D. cucullata*. Mean relative helmet length (%) + 1 SE are shown. Two body-length size classes (sc2 = 600–800  $\mu\text{m}$ ; sc3 = 800–1000  $\mu\text{m}$ ) were used for analysis. Asterisks indicate significant differences between the treatments (\*\*\*) =  $p < 0.001$ ). The differences to the control were significant ( $p < 0.001$ ) in all cases.

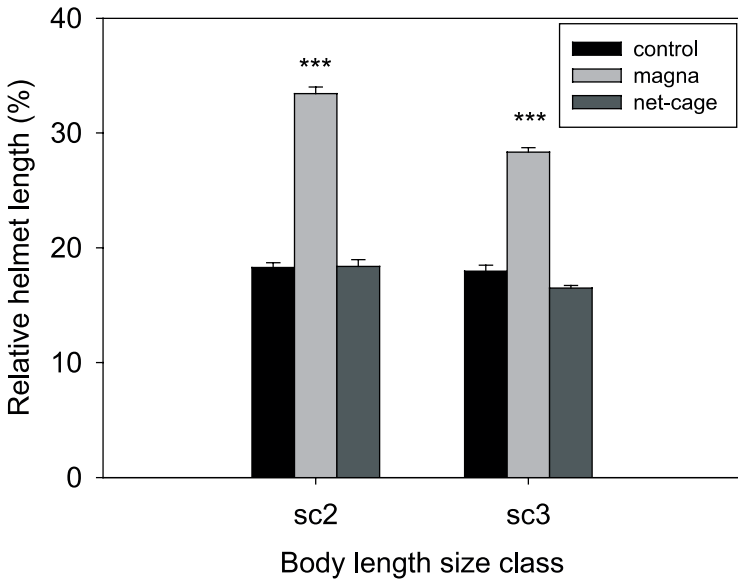
## Results

### Artificial turbulence and kairomones

A clear synergistic effect of predator kairomones and turbulence was revealed by this experiment. Helmet length of *D. cucullata* differed significantly between treatments in both body-length size classes (nested ANOVA: sc2:  $F_{3,8} = 76.27$   $p < 0.001$ , sc3:  $F_{3,8} = 46.03$   $p < 0.001$ ). Helmets of *D. cucullata* were significantly longer in all induction treatments compared to the control (Tamhane Post-Hoc Tests: all  $p < 0.001$ , Fig. 2). Tamhane multiple-comparison tests show that the helmets of *D. cucullata* exposed to turbulence and predator kairomones simultaneously were significantly longer compared to both single-stressor treatments (sc2, sc3:  $p < 0.001$ ). Helmet length of *D. cucullata* did not significantly differ between animals exposed to either just turbulence or predator kairomones alone.

### Turbulence evoked by *Daphnia magna*

Turbulence generated by movements of *D. magna* induced significantly longer helmets in *D. cucullata* in both body-length size classes (nested ANOVA: sc2:

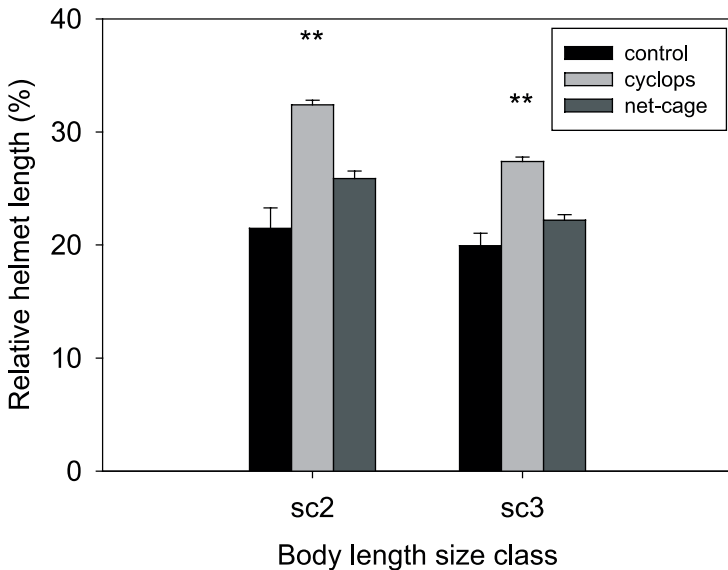


**Fig. 3.** Turbulence generated by swimming *D. magna* in direct contact (magna) induced significantly larger helmets compared to a net-cage treatment which shielded *D. cucullata* from hydrodynamic cues from *D. magna* (net-cage) and a control. Mean relative helmet length (%) + 1 SE of *D. cucullata* in two body-length size classes (sc2 = 600–799  $\mu\text{m}$ ; sc3 = 800–1000  $\mu\text{m}$ ). Asterisks indicate significant differences between the treatments (\*\*\* =  $p < 0.001$ ).

$F_{2,6} = 51.34$   $p < 0.001$ , sc3:  $F_{2,7} = 162.15$   $p < 0.001$ ; Tamhane Post-Hoc Tests: all  $p < 0.001$ , Fig. 3). The *Daphnia* which received only chemical cues released by *D. magna* as the inducing agent (net-cage) showed no significantly higher helmets compared to the control.

### Kairomones and turbulence evoked by predatory copepods

Direct contact between *Cyclops* and prey, leading to the exposure of prey animals to turbulence evoked by moving predators and released chemicals simultaneously, induced significantly longer helmets in *D. cucullata* compared to the control treatment (nested ANOVA: sc2:  $F_{2,6} = 16.62$   $p = 0.003$ , sc3:  $F_{2,5} = 8.47$   $p = 0.02$ , Fig. 4). Tamhane multiple-comparison tests show that helmets of *D. cucullata* induced by direct contact were significantly longer compared to both kairomone (net-cage) and control treatment (sc2: cyclops vs control  $p = 0.005$ ; cyclops vs net-cage  $p < 0.001$ ; sc3: cyclops vs control  $p = 0.001$ ; cyclops vs net-cage  $p < 0.001$ ). No significant difference was detected between the control and the net-cage treatment under these conditions.



**Fig. 4.** *D. cucullata* in direct contact to *Cyclops* sp. and exposed to turbulence and chemical cues from *Cyclops* sp. simultaneously (cyclops) formed significantly larger helmets compared to a control treatment and a treatment in a net-cage where only chemical cues could pass (net-cage). Mean relative helmet length (%) + 1 SE are shown. Two body-length size classes (sc2 = 600 – 799  $\mu\text{m}$ ; sc3 = 800 – 1000  $\mu\text{m}$ ) were used for analysis. Asterisks indicate significant differences between the treatments (\*\* =  $p < 0.01$ ).

## Discussion

Synergistic effects on organisms have been shown for a variety of external factors. Especially well studied are toxicological influences where sublethal effects of individual substances sum up in an additive or non-additive way. Our experiments revealed that synergistic effects between chemical cues and mechanical cues exist for morphologically plastic traits in *D. cucullata*. This observation should be relevant for explaining helmet formation in nature because the single cues might rarely occur in the relevant strength to induce maximal sized traits. We report in another paper (LAFORSCH et al. 2006) that predator kairomones and chemical alarm cues released by crushed conspecifics can induce helmet formation. Thus, it seems likely that phenotypic plasticity in helmet length in *Daphnia* is a multi-factorial phenomenon, where several proximate factors act synergistically to induce the traits.

We have previously shown (LAFORSCH & TOLLRIAN 2004 b) that strong turbulence can induce the maximal sized helmets in *D. cucullata* under lab conditions. But what is the natural source of the inducing turbulence and what is the ultimate advantage of helmet formation in turbulent conditions? We found that



two different populations of *D. cucullata*, from neighbouring lakes of similar morphometry, produced different helmet sizes in the field, but were equally reactive when tested in the lab (LAFORSCH & TOLLRIAN 2004b). Wind-induced turbulence should have been rather similar in both lakes. Furthermore, it is reasonable to assume that wind-induced turbulence should be strongest during the stormy periods in spring and autumn, when the lakes are mixed, which does not match the pattern of cyclomorphosis with the higher helmets occurring in summer (LAMPERT & WOLF 1986). Thus, it seems unlikely that wind-induced turbulence is the inducing cue in natural systems. Possibly, there is a biotic source for the inducing small-scale turbulence. Our experiment using copepods as predators indeed suggests that predator movements might create the hydromechanical cues. *D. cucullata* in direct contact with the predators formed significantly higher helmets compared to animals which had been in a net-cage in the same tank. We had tested that the net-cage reduced or eliminated the turbulence but allowed the chemical cues to pass. Thus, the *Daphnia* in direct contact received both, mechanical and chemical stimuli, while the caged *Daphnia* received only chemical cues. However, we can not rule out that bacteria settled on the net-cages. These might have broken down the kairomones, meaning that our observation was not caused by the influence of mechanical cues but merely by different concentrations of chemical cues. As long as the kairomones have not been identified it will not be possible to measure their concentration directly. However, there is some evidence against this argument. The net-cages were constructed using 100  $\mu\text{m}$ -gauze and regularly cleaned. We did not observe a clogging of the gauze nets, which might indicate bacterial growth or a severe diffusion barrier. Diffusion will not have been affected, as we maintained the same predator densities for three weeks and an equal concentration within and outside the cages should have established rapidly. The same type of net-cage has been used routinely to enclose predators which release chemical cues into the surrounding tank, which always provided a transfer of chemicals. The strongest argument in favour of a mechanical cue however, comes from our experiment with *D. magna*. Here we also measured significant helmet formation, but found no chemical induction. Chemical induction was also not to be expected, as *D. magna* does not release any inducing chemical cues, beside alarm cues (LAFORSCH et al. 2006) which did not occur in this treatment. Similarly, direct selection is an unlikely explanation. First, we used a single clone which does not show this range of variation of the trait in control conditions. Second, the *D. magna* treatment rules out direct selection as there was no predation.

The reason why we did not measure significant helmet induction by chemical cues from copepods, despite our previous results (LAFORSCH & TOLLRIAN 2004a), might be explained by a lower concentration of inducing chemicals. We did not control for high food levels for the predators in this study because

we were interested in a difference between chemical cues and chemical cues in combination with turbulence, which we could demonstrate successfully.

The result that *D. cucullata* respond to mechanical stimuli produced by non-predacious heterospecifics indicates that the information content provided by the mechanoreceptors is unspecific. This is similar to broadly defined unspecific alarm cues released by crushed *Daphnia* which have been shown to be sensed by *D. magna* (PIJANOWSKA 1997, PIJANOWSKA & KOWALCZEWSKI 1997), *Daphnia galeata* (STABELL et al. 2003) and several other *Daphnia* species including *D. cucullata* (LAFORSCH et al. 2006). These unspecific chemical cues and unspecific mechanical cues together with more specific predator kairomones might provide a relatively accurate source of information about the actual predator environment. Because inducible defences evolve in a cost-benefit framework (TOLLRIAN & HARVELL 1999), the quality of information about the environment is relevant for avoiding costs associated with the formation of defences (GABRIEL et al. 2005, GABRIEL 2006, this volume).

The suggestion that invertebrates produce small-scale turbulence which induces helmet formation in *D. cucullata* would directly link turbulence induction and kairomone induction to predator recognition and to a defensive function as ultimate reason and thus helps to explain this old phenomenon.

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