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An overview of the contribution of studies with cladocerans to environmental stress research

Um panorama da contribuição de estudos com cladóceros para as pesquisas sobre o estresse ambiental

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Abstract: Cladocerans are microcrustaceans component of the zooplankton in a wide array of aquatic ecosystems. These organisms, in particular the genus *Daphnia*, have been widely used model organisms in studies ranging from biomedical sciences to ecology. Here, we present an overview of the contribution of studies with cladocerans to understanding the consequences at different levels of biological organization of stress induced by environmental factors. We discuss how some characteristics of cladocerans (e.g., small body size, short life cycles, cyclic parthenogenesis) make them convenient models for such studies, with a particular comparison with other major zooplanktonic taxa. Then we illustrate the contribution of cladocerans to stress research with examples encompassing stress responses spanning from the molecular to the populational level. Most worth of note are recent studies that presented evidence of beneficial consequences of mild stress caused by natural stressors (cross-tolerance), which may be passed along across generations, favoring individual survival and species persistence in fluctuating environments. This would be particularly relevant for environments prone to frequent natural environmental fluctuations, such as coastal lagoons and other shallow aquatic ecosystems. Based on reviewed studies, a conceptual model is presented summarizing the potential effects of a first stressor on the organism's resistance to a second one. We finish by highlighting some gaps on environmental stress research that could benefit from further studies using cladocerans as model organisms.

Keywords: Cladocera; stress; cross-tolerance; ecotoxicology; ecophysiology.

Resumo: Os cladóceros são microcrustáceos integrantes do zooplâncton em um vasto espectro de ambientes aquáticos. Estes organismos, em especial o gênero *Daphnia*, têm sido organismos modelo muito utilizados em estudos abrangendo das ciências biomédicas à Ecologia. No presente trabalho, fazemos uma revisão da contribuição de estudos com cladóceros para o conhecimento sobre as consequências, em diferentes níveis de organização biológica, do estresse induzido por fatores ambientais. Discutimos de que forma características peculiares dos cladóceros (e.g., pequeno tamanho corporal, ciclo de vida curto, partenogênese cíclica) fazem deles modelos bastante convenientes para tais estudos, com uma comparação particular com outros grandes grupos zooplanctônicos. Em seguida, ilustramos a contribuição dos cladóceros para as pesquisas sobre estresse com exemplos englobando respostas ao estresse do nível molecular ao populacional. São ressaltados de forma especial estudos recentes que apresentam evidências de consequências benéficas do estresse brando causado por estressores naturais (tolerância cruzada), as quais podem ser transmitidas entre gerações, favorecendo a sobrevivência e a persistência de espécies em ambientes muito variáveis. Isto seria particularmente relevante para ambientes sujeitos a frequentes variações naturais intensas, tais como lagoas costeiras e outros ecossistemas aquáticos rasos. Com base nos estudos revisados, construímos um modelo conceitual resumindo os potenciais efeitos de um primeiro estressor na resistência dos organismos a um estressor subsequente. Concluímos chamando a atenção para algumas lacunas nas pesquisas sobre o estresse em contexto ambiental, as quais poderiam ser preenchidas por estudos futuros utilizando cladóceros como modelos.

Palavras-chave: Cladocera; estresse; tolerância cruzada; ecotoxicologia; ecofisiologia.

1. Introduction

In the ecological literature, particularly within Ecophysiology, stress has been a recurrent theme. Organisms are constantly subject to variation in their environment, and many of these varying factors act as stressors, displacing the organisms from their fundamental niches (Van Straalen, 2003; Steinberg, 2011). Besides natural stressors, human-induced environmental changes—among which, the increasing chemical pollution of ecosystems—represent important sources of stress in the environment. Most of the understanding of how stress affects organisms comes from studies with model organisms that are small enough to be cultivated and used in short-term experiments in the laboratory. Among the most popular model organisms in Biology are the *Drosophila* fruitflies, the clawed frog *Xenopus laevis* and the nematode *Caenorhabidits elegans* (Seda & Petrusek, 2011).

In aquatic ecosystems, zooplanktonic organisms have been widely used as models for studies testing and developing ecological theories, as reviewed by Lampert (1997). Among the examples cited therein are studies on mechanistic models of competition (Rothhaupt, 1988) and inducible phenotypic changes (Taylor & Gabriel, 1992). Short life cycles, small body size and their central role in pelagic food webs are some of the main features that make zooplanktonic organisms so suitable for such studies. One specific group within zooplankton—namely the crustacean order Cladocera—has received special attention across ecological studies, in particular those dealing with environmentally-induced stress from its many perspectives (e.g., biochemical, molecular, physiological, toxicological).

Cladocera have peculiar biological features that make their use in experimental studies very appealing. Moreover, cladocerans may be found in highly fluctuating environments, such as ponds and shallow coastal lagoons (Petrusek, 2002; Santangelo et al., 2008; Dodson et al., 2009), making them even more interesting models for research on environmental stress. Among cladocerans, the genus *Daphnia* receives special attention from researchers due to its widespread distribution, especially in temperate regions (Sarma et al., 2005). *Daphnia* species, particularly *Daphnia magna,* have become important model organisms for studies ranging from biomedical sciences to ecology, but they share several ecological features with other cladocerans that offer similar advantages (Ebert, 2011; Seda & Petrusek, 2011; Miner et al., 2012).

In this review, we aim to present an outlook of the contribution of cladoceran studies to environmental stress research. First, we briefly discuss the definition of stress in the light of recent, challenging findings regarding the effects of *mild stress*. Then, we present a brief description of cladoceran biology, highlighting some of the reasons for their prevalence over other zooplanktonic groups in studies about stress. We follow with a set of examples of cladoceran studies using different approaches (e.g. biochemistry or life table experiments) to address the consequences of stress to organisms. We finish by considering some gaps that may be filled up with the use of cladocerans, which could contribute to the advance of stress research in a pure ecological point of view, as well as in the context of ongoing natural and human-induced changes experienced by ecosystems.

2. Defining Stress

The term stress, much alike other highly pervasive terms in Ecology—e.g., adaptation, disturbance—may have as many definitions as there are sub-disciplines and methodological approaches to address it. It is not our aim here to discuss in depth the definition of stress (for reviews, see Parker et al., 1999; Bijlsma & Loeschcke, 2005). Nevertheless, we wish to derive a consensual definition of stress based on recent debates in the literature, before we proceed to present and discuss the reviewed studies.

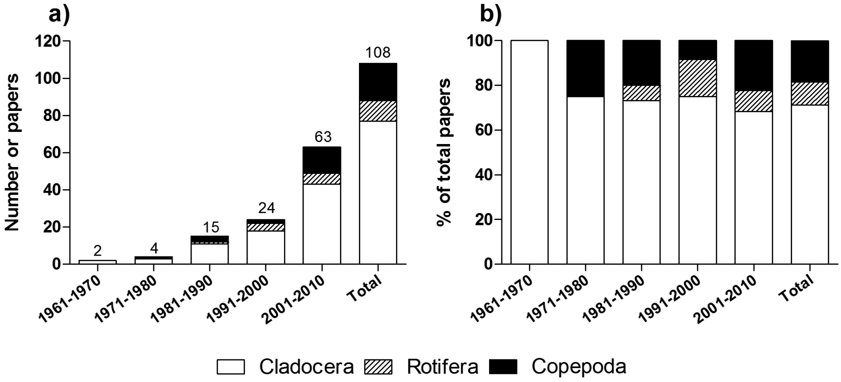

Figure 1. Scientometric analysis of the contribution of studies with the major zooplanktonic taxa to the research on stress, highlighting the prevalence of cladocerans over rotifers and copepods in number (a) and percentage (b) of published papers. For details on the methods used for the survey, please refer to the footnote[1].

Stress is the state experienced by an organism when it is challenged by abiotic and/or biotic changes in its environment (stressors), which translate into a set of identifiable symptoms (stress responses), mostly at the suborganismal level, e.g. biochemical and molecular levels (Parker et al., 1999; Van Straalen, 2003). Some of these symptoms are quite general and unspecific, regardless of the nature of the stressor, such as the development of oxidative stress and induction of repairing proteins (the so-called *heat shock proteins*, HPSs) (Steinberg, 2011). This gave rise to the use of many enzymes and proteins, and ultimately the expression of the genes coding for them, as stress biomarkers (Steinberg et al., 2008b). The development of the "-omic" approaches—i.e., the mapping of whole-proteomic, -genomic and -metabolomic expression in organisms—led to sensitive and comprehensive methods for evaluating the effects of stress in organisms (Bijlsma & Loeschcke, 2005; Steinberg et al., 2008b).

However, as we shall further depict with some cladocerans' examples, the ultimate effects of stress at the organismic and higher levels of biological organization seem not to fit into the classical paradigm of stress as something necessarily detrimental (see Steinberg, 2011 for a thorough review). Challenging findings in the last two decades made obvious that stress in a mild range—which is frequently exerted by regular, day-by-day, natural stressors in ecosystems—may turn out to be beneficial to the overall fitness of organisms, even though they show typical stress symptoms (Minois, 2000; Steinberg et al., 2008a; Suhett et al., 2011). Exposure to mild stress would stimulate the stress defense systems, improving the performance of organisms against further stressors (Minois, 2000). Put this way, stress is seen as a fundamental aspect of life itself and, being an ever-acting environmental and evolutionary force, not only at the "harsh stress – detrimental effects" range (Steinberg et al., 2006; Steinberg, 2011).

3. Why Cladocerans?

We performed a scientometric survey[1] considering the publications on stress which used the three major zooplanktonic taxa—namely the crustacean order Cladocera and subclass Copepoda and the phylum Rotifera—as model organisms. The survey, which covered 108 papers published from 1961 to 2010, revealed that Cladocera have been the most prominent taxon, accounting for 71% (84 papers) of the total papers, followed by Copepoda (19%, 23 papers) and Rotifera (10%, 14 papers) (Figure 1). The prevalence of Cladocera over the other taxa was consistent throughout the analyzed period, accounting for 68 to 100% of the papers analyzed for each decade (Figure 1b). Additionally, we should highlight that the genus *Daphnia* was also prevalent among cladocerans, being present alone in 98% of the papers with

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[1] The survey was performed using the ISI Web of Science® database and papers from 1961 (oldest record found with the used keyowrds) to 2010 were considered. Our approach was conservative, constraining the keyword search to the article titles. The search criteria entered were the following, according to each taxon: 1) Cladocera: stress AND cladocer* OR stress AND daphnia OR stress AND moina; 2) Rotifera: stress AND rotifer* OR stress AND brachionus; 3) Copepoda: stress AND copepod* OR stress AND calan*. The genera names used as keywords for each taxon were chosen after a preliminary analysis, which has shown that they were representative of those taxa. In the case of Copepoda, "calan*" applied to both the genus *Calanus* and to the order Calanoida as a whole.

cladocerans (data not shown). The number of papers relating the three zooplanktonic taxa and stress increased exponentially from 1961 to 2010, but this may simply reflect an increase in the number of scientific publications as a whole.

The reasons for the prevalence of cladocerans lie in peculiar features of their biology, which make them particularly convenient models for experimental studies (Edmondson, 1987). Indeed, cladocerans are among the oldest test organisms and have been used by C. L. Naumann in the 1930's (Andersson 1980 apud Baudo, 1987). Cladocerans have a wide geographical distribution, with a broad range of forms, physiological and ecological traits (Threlkeld, 1987). They occur in ecosystems ranging from small puddles to large lakes, assuming a central role in the food webs in many of these ecosystems (de Bernardi & Peters, 1987). Cladocerans are generally easy to sample and to keep in laboratory cultures and they have short generation times (2 to 10 days) and mean lifespan (4 to 150 days) (Lynch, 1980; Sarma et al., 2005). They are also relatively small (usually less than 3 mm), demanding little space for being cultivated (Sarma et al., 2005), but they are still visible to the naked eye and not as small as rotifers, being easily handled in experiments with simple instruments. Moreover, their fast and prolific reproduction, with clutch sizes that often exceed 20 neonates per clutch (Lynch, 1980), makes them easily available in enough numbers for ecological experiments in a short time scale (Miner et al., 2012).

Different from copepods, which only reproduce sexually, cladocerans reproduce mostly asexually via parthenogenesis, similarly to rotifers (Figure 2). When they experience stressful situations, such as food shortage, changes in food quality and crowding, parthenogenetic females produce male offspring and initiate the sexual production of resting eggs that may wait for decades for favorable conditions to hatch, beginning a new parthenogenetic population (Gyllström & Hansson, 2004; De Meester et al., 2006; Koch et al., 2009). Thus, increased production of male offspring and the switch to sexual reproduction are a typical functional response of cladocerans to the stress caused by many environmental factors.

Additionally, the clonal reproduction of cladocerans brings three major advantages to research on stress in an ecological context. First, experiments can be controlled for genetic variation. Second, it allows for testing specifically for maternal transgenerational effects of stress, which are more complex to study in obligatory sexual animals. Finally, different clones may respond differently to stress, and this represents an interesting scope for understanding the relationships between genotypes and phenotypes under stress, because multi-clonal populations represent more discrete "packed" genotypes as compared to populations of organisms that reproduce only via sexual reproduction, where genetic flux is constant.

For the above reasons, cladocerans are very popular and appropriate model organisms for studies on the consequences of stress at different levels of biological organization, particularly those spanning from genes to populations, encompassing short-term ecotoxicogenomic and ecotoxicological tests or whole-lifespan life table experiments, as we shall exemplify in the next sections. Nevertheless, we should be aware of the limitations imposed by peculiarities of cladoceran biology—such as the prevalence of assexual clonal reproduction—when trying to generalize these findings (Threlkeld, 1987).

4. Multiple Perspectives on Stress Responses and Approaches at Different Organization Levels

4.1. Biochemical and molecular stress responses

Biochemical assays, such as those for measuring enzyme activity or quantifying proteins (e.g. HSPs) suffer a limitation from the needed amount of biological material. This means that these methods are not so easily applied for small organisms if one wishes to use them with a large number of experimental replicates. For this reason, the application of such direct methods for cladocerans is not much worthy due to sensitivity problems. However, one integrative method for evaluating the total oxygen scavenging capacity (TOSC) of samples—i.e., their global oxidants/anti-oxidants

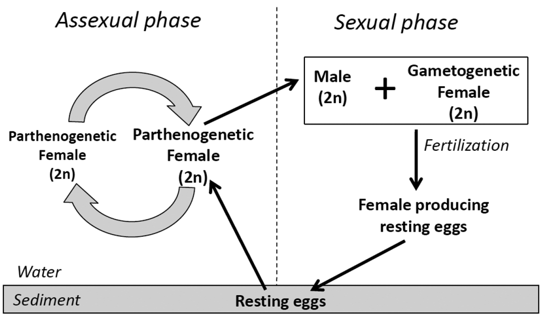

Figure 2. The reproductive cycle of cladocerans (After De Meester et al., 2006).

balance—has been successfully applied for *Daphnia magna* and even to the smaller *Moina macrocopa* exposed to natural chemicals (Steinberg et al., 2010a; Hofmann et al., 2012; Engert et al., 2013). This approach seems more informative and relevant for understanding the effects of stress in organisms than measuring single oxidant species or anti-oxidant enzymes (Steinberg et al., 2010a), and it could be further applied to cladocerans in other ecological contexts.

Molecular techniques, on the other hand, are much more sensitive due to the possibility of replicating DNA in PCR (polymerase chain reaction) assays, amplifying the signal to be measured (Chen et al., 1999). It must be noted here, however, that transcripts reflect a potential stress response, whereas proteins and metabolites show the actual response and its pathways. Transcripts are often modified or destroyed during translation to the mitochondria.

Practically, the transcripts (mRNA) of genes coding for the above mentioned enzymes and proteins may be transformed to cDNA, and quantified as an indirect measure of these stress biomarkers. Using these techniques, for example Chen et al. (1999) show an increased expression of HSP 83 in *Daphnia pulex* when exposed to arsenic. Steinberg et al. (2010a) evidence the induction of the genes coding for HSP 60 and catalase (an anti-oxidant enzyme) in *D. magna* by poor food quality and exposure to humic substances.

The advance of genomic techniques brought up new methods for multivariate gene-expression analysis (DNA microarrays and mRNA sequencing) encompassing virtually thousands of genes. With these techniques, one may observe simultaneously which genes are up- and down-regulated when organisms are submitted to stress (Steinberg et al., 2008b). This approach has been used with cladocerans mostly from an ecotoxicological perspective—the so called *ecotoxicogenomics*—i.e., testing the effects of chemicals on the overall gene activity profile of organisms exposed to toxicants (Vandenbrouck et al., 2011). However, recent studies with *Daphnia* have used genomic techniques to identify genes involved in the regulation of two key aspects of cladoceran life cycle, namely male offspring production and predator-induced defenses (Eads et al., 2008; Spanier et al., 2010). Interestingly, these studies with *Daphnia* challenge the current paradigm of stress genes being highly conserved, because a high proportion of the stress-responsive genes in *Daphnia* seem to be exclusive for the genus (Eads et al., 2008; Colbourne et al., 2011). Recent genetic studies with *D. pulex* also reveal an elevated rate of gene duplication, with the presence of several copies (paralogs) of the same gene (Colbourne et al., 2011; Asselman et al., 2012). This phenomenon has been associated in evolutionary research to adaptive mechanisms to the persistence of species in highly changing environments (Zou et al., 2009; Kondrashov, 2012). We do not know yet any similar comprehensive genetic study for other cladoceran species. But the latter species, at least, seems to be a good candidate to evolutionary studies focusing on organisms experiencing harsh and fluctuating environments.

4.2. Traditional ecotoxicological tests: acute and chronic toxicity

Cladocerans, particularly *Daphnia*, are probably the most used organisms in ecotoxicological tests. There is a vast literature on the effects of metals, organic pollutants and natural toxicants on these organisms (for review, see Sarma & Nandini, 2006). Acute tests evaluate the effects of chemicals at short time scales (usually 1-3 days), mostly in mortality or motility tests. The LC_{50} is the major variable derived from these tests, representing a concentration of the chemical which is lethal to 50% of tested organisms. Chronic toxicity is measured at time scales that integrate the effects of chemicals to the growth and reproduction of organisms, and their time span will depend on the lifespan of the respective species. Survival and reproductive rates are the main response variables in these assays (Chen et al., 1999; Ferrão-Filho et al., 2009).

We shall not list specific cases of toxicants and their effects. Rather, we wish to highlight recent studies that evaluate how toxicity of chemicals is affected by other environmental factors and by the ontogenetic stage (e.g., newborns *vs.* adults). For example, recent studies have evaluated how temperature modulates the effects of endocrine disruptors in *Moina micrura* (Miracle et al., 2011), and of nickel (Vandenbrouck et al., 2011) and filamentous cyanobacteria in *D. magna* (Bednarska et al., 2011). In another example, Ferreira et al. (2010) tested how temperature and dissolved oxygen extremes and food shortage affect nickel toxicity, and their results show that predicting toxicity in more variable, ecologically realistic contexts is not a straightforward question (Ferreira et al., 2010). We shall further discuss this "multiple stressors" issue in another section.

Studies comparing the sensitivity of young (newborns) and adult cladocerans have shown that adults are in general less sensitive to the stress exerted by heavy metals or genotoxic substances (Chen et al., 1999; David et al., 2011). This pattern of differences in sensitivity was apparent for both demographic (longevity and fecundity) and biochemical aspects (expression of stress proteins), the latter being more responsive (Chen et al., 1999). As highlighted by David et al. (2011), the expression of DNA repair genes in *D. magna* due to stress is more intense in adults. Thus, these studies call attention to the relevance of considering different life stages in ecotoxicological tests.

Overall, the studies mentioned above add new dimensions to traditional ecotoxicological approaches, bringing more environmental realism and relevance to ecotoxicological tests.

4.3. Inducible phenotypic responses to predation stress

The perception of predators also causes stress symptoms in cladocerans, which are evident at the molecular and biochemical levels and cause several inducible phenotypic changes (Agrawal et al., 1999; Slos & Stoks, 2008). *Daphnia* species—such as *D. magna*, *D. pulex*— are perhaps the most emblematic examples of phenotypic plasticity in aquatic ecology. Their innate seasonal cyclomorphosis and their predator-induced morphological changes are a very appealing case for studies on phenotypic plasticity (Edmondson, 1987; Simon et al., 2011). Macháček (1991) was likely the first to evidence life history changes in cladocerans due to stress induced by chemical cues from predators. In this study, the presence of a fish predator reduzed *Daphnia galeata* body and egg size, which were related to a faster sexual maturation of neonates (Macháček, 1991). Chemical cues from invertebrate predators (*e.g.*, the phantom midge *Chaoborus*), on the other hand, induce somatic growth and the appearance of conspicuous body shapes with helmets, neckteeth and spines to escape predation (Agrawal et al., 1999; Lass & Spaak, 2003). Pijanowska & Kloc (2004) shed light the intracellular mechanism behind those responses to vertebrate and invertebrate predators, which involve induction of stress proteins (HSPs) and even structural changes in the actin and tubulin cytoskeleton.

A recent study by Rabus & Laforsch (2011) with *D. magna* shows evidence that a prey may switch between plastic defense traits from juvenile to adult stages to maintain effective defense throughout their whole lifetime. As highlighted by the authors, these results represent a novel and complex functionality of inducible defenses (Rabus & Laforsch, 2011). Another recent study worth to note shows that endocrine disrupting pesticides that mimic the major crustacean hormone methyl farnesoate interfere with the morphological plasticity of *D. galeata*, which may have important consequences for predator-prey interactions in increasingly polluted aquatic environments (Oda et al., 2011).

Due to their clonal reproduction, cladocerans are good models for providing evidence that predator-induced changes may also be transmitted to the offspring via maternal effects (Agrawal et al., 1999; Pijanowska & Kloc, 2004). Nevertheless, for smaller species, such as *M. micrura*, increasing body length and changing the shape may not be an effective strategy; rather, these organisms respond by increasing offspring numbers (Santangelo et al., 2011). Thus, evolutionary and developmental constraints imposed by small body size prevent the formation of some types of defense. Predator-induced changes in shape and life history traits have also been shown to vary across broods and generations (Agrawal et al., 1999; Santangelo et al., 2011).

4.4. Whole life table experiments

As said above, cladocerans are very suitable for studies encompassing the whole lifespan in a short time scale. Whole-lifespan life table experiments are quite informative, because one can have an integrated overview of the effects of stress on organisms, in contrast to the one-sided view that one would have by simply counting the offspring or measuring mortality in toxicity tests.

We illustrate that by an example (Figure 3) with *M. macrocopa* exposed to aquatic humic substances (HSs), which act as a mild stressor at environmentally realistic concentrations (Suhett et al., 2011). Although clearly stressed by humic substances (increased male offspring production, Figure 3c), *M. macrocopa* responds with increased somatic growth (Figure 3a), fecundity (Figure 3b) and lifespan (Figure 3d) at low HSs concentration, but the two latter stimuli fade out at higher HSs concentration (Figure 3b and d). These results show how a multi-faceted life table approach may give novel insights into the ultimate outcomes of stress to life history, because energetic trade-offs take place in the management of stress responses and vital functions by organisms along stress gradients.

Another interesting aspect evidenced by such studies is that the response of organisms' life history may be contrasting depending on the specific stressor applied (Table 1). For example, the osmotic stress caused by increasing salinity leads to reduced somatic growth, fecundity and longevity and retards the sexual maturation in cladocerans (Martínez-Jerónimo & Martínez-Jerónimo, 2007; Santangelo et al., 2008). Food shortage or reduced food quality reduce only the somatic growth and fecundity, but elongate their lifespan and retard the onset of reproduction (Ferrão-Filho et al., 2003; Xi et al., 2005; Bouchnak & Steinberg, 2010). Temperature increases, on the other hand, reduce longevity and somatic growth, but accelerate sexual maturation and increase fecundity in cladocerans to some degree (Folt et al., 1999; Xi et al., 2005; Engert et al., 2013). Experiments with cladocerans that try to evaluate multiple life history traits, combining different stressors, may largely contribute to understanding how organisms deal with the often contrasting effects of those stressors at more environmentally realistic scenarios.

4.5. Multiple stressors: do they always act synergistically?

As pointed out above for ecotoxicological research, putting stressors together in more environmentally realistic scenarios is mandatory for relevant research on the consequences of stress to organisms in nature. In the literature, we can find several examples of synergistic detrimental effects of stressors, many of them with well designed factorial experiments and multiple life history response variables (e.g., somatic growth, fecundity and lifespan). For instance, Coors et al. (2008) found enhanced virulence of parasites by co-exposure to the pesticide carbaryl in *D. magna*. A synergistic interaction was also observed for salinity and temperature in *Daphniopsis australis*, with stronger salinity effects at lower temperatures (Ismail et al., 2011).

Nevertheless, recent studies with mild stressors challenge the paradigm that "all stress is stressful" and that combined stressors always act synergistically leading to reduced fitness (Steinberg, 2011). Some

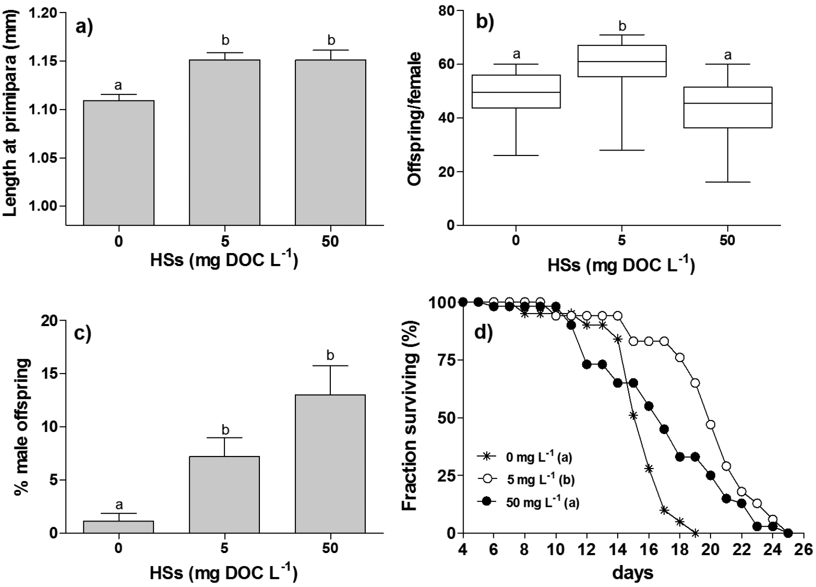

Figure 3. An example of a whole-lifespan life table experiment with *Moina macrocopa* exposed to different concentrations of humic substances (HSs = 0, 5 and 10 mg dissolved organic carbon L^{-1}). a) Body length at primipara (sexual maturity), b) total offspring per female, c) % of male offspring per female and d) Survival curves. Different lower-case letters denote statistical differences between treatments (Modified from Suhett et al., 2011).

Table 1. Summary of the consequences of stress caused by different environmental factors (stressors) to specific life history traits of cladocerans.

	Longevity	Somatic growth	Sexual maturation	Fecundity
Salinity	-	-	-	-
Food shortage	+	-	-	-
Temperature increase	-	-	+	+

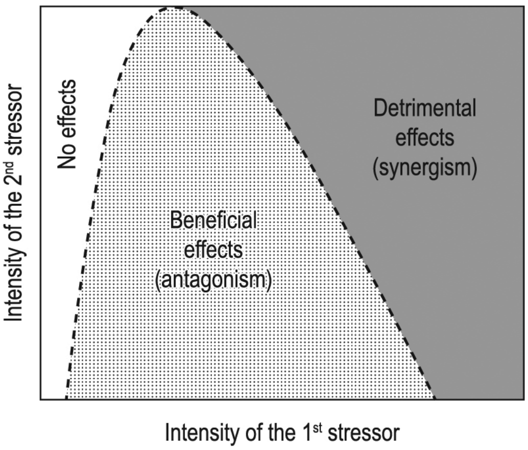

Figure 4. A conceptual model of the overall effects of exposure to two stressors sequentially and cumulatively. Exposure to a 1st stressor at low to medium intensities, by exerting a mild stress, may activate stress defense systems, rendering the organism more resistant to a 2nd stressor (dotted area). These effects would be observed only above a threshold intensity of the 1st first stressor, bellow which stress defense mechanisms would not be effectively activated (white area). In situations of higher intensities of the stressors, the overall energetic cost of stress would level off the possible beneficial effects of the 1st stressor, leading to synergistic detrimental effects of both stressors (shaded area). Above a given intensity, the stress caused by the 1st stressor becomes energetically costly, hindering the occurrence of beneficial effects. Irrespective of the intensity of the 1st stressor, the increase in intensity of the 2nd stressor always reduces the probability of beneficial effects of exposure to the 1st stressor.

of the most recent results in this way came from studies with cladocerans. Although HSs induce oxidative stress in *D. magna*, this mild stress is able to alleviate stress symptoms caused by poor food quality (yeast) in cross-exposure treatments (Bouchnak & Steinberg, 2010; Steinberg et al., 2010a). Much in the same way, *M. macrocopa* individuals presented an alleviation of salt-induced reduction in somatic growth when co-exposed to natural HSs, even though these substances caused stress symptoms in isolated exposure (Suhett et al., 2011). Additionally, this stress resistance (or cross-tolerance) induced by mild stress was transmitted transgenerationally to the offspring, which were more resistant to salt even when HS were present to mothers only (Suhett et al., 2011).

In a recent paper, Engert et al. (2013) have shown that any temperature outside the thermal optimum induced stress, indicated by reduced antioxidant capacities, in *M. macrocopa*. However, if exposed to HSs, the water fleas respond with increased body size, lifespan, and offspring numbers when slightly above its temperature optimum. A convincing explanation appears to be the mitohormesis hypothesis which states that a certain increase of reactive oxygen production leads to improved health and longevity (Ristow & Zarse, 2010; Ristow & Schmeisser, 2011) and, with *M. macrocopa*, also to increased offspring numbers. This indicates that this cladoceran species seems to benefit from increasing temperature slightly above its thermal optimum.

Based on these recent results with cladocerans, we propose a simplified conceptual model of the effects of multiple stressors (Figure 4), considering a scenario of exposure of the organism to two stressors sequentially and cumulatively. This scenario is representative, for example, of a coastal lagoon with fluctuating HSs content and subject to occasional salinity increases due to marine intrusions and storms (Caliman et al., 2010). The shaded area in the graph represents the combinations of intensities of both stressors upon which the organism would not benefit from the exposure to the first stressor for acquiring resistance against the second one. Under those conditions, the upcoming energetic demands are overwhelming in the final balance, and this is the scenario most commonly found in studies on stress, with synergistic detrimental effects of multiple stressors. Above a certain intensity of the first stressor, this would be by itself too harsh, not rendering the organisms more resistant to further stressors (Figure 4). The dotted area represents the combinations of intensities where the first stressor would be efficient in promoting resistance against the second one, due to the "training" of stress defense systems (Figure 4). This pattern would be closely related to the phenomenon of hormesis, which describes positive effects of toxic compounds and other stressors at low doses to fitness parameters, while detrimental effects show up with the progressive dose increase (Calabrese & Baldwin, 2003). The positive effects of the first stressor would take place only above a threshold intensity, bellow which this stressor would not be effective in stimulating the stress defense systems (white area, Figure 4). In general, the higher the intensity of the second stressor, the less likely are the beneficial effects (*i.e.*, stress resistance) against the second one (narrowing of the dotted region, Figure 4), irrespective of the intensity of the first stressor. The dotted area in the graph represents the situations where mild stress—which is certainly a present factor at environmentally realistic conditions—promotes resistance of organisms to multiple stressors. Under these situations, mild stress would be an important component of the ability of species to survive and persist at ecological and evolutionary timescales (Steinberg, 2011; Suhett et al., 2011).

4.6. Stress effects across generations: the message from epigenetics

From an ecological and evolutionary point of view, it is fundamental to understand the impact of stress beyond the generation that is being particularly exposed to a stressor. As shown above, it is clear that the offspring response to stress is influenced by the exposure of mothers (Agrawal et al., 1999; Suhett et al., 2011). But which are the mechanisms through which this transgenerational communication happens? Epigenetic inheritance—*i.e.,* chemical and conformational changes in DNA and chromatin without alteration of nucleotide sequence—has been evidenced as a potential mechanism accounting for maternal effects, reviving the debate on soft inheritance of acquired characters (Bossdorf et al., 2008; Ho & Burggren, 2010). Recent studies with cladocerans show that exposure to metals (Vandegehuchte et al., 2009; Vandegehuchte et al., 2010) and HSs (Menzel et al., 2011) induce DNA methylation, a major epigenetic mechanism. Thus, epigenetic inheritance is a strong candidate for explaining transgenerational effects of stress in cladocerans. Nevertheless, the stability of epigenetically inherited changes over generations is still hotly debated, especially when sexual reproduction takes place, because DNA methylation does not necessarily overcome meiosis (Ho & Burggren, 2010). However, if an epigenetic mechanism is passed to succeeding generations, it can act like a mutation (Sollars et al., 2003).

Although we do have evidences that past stress influences the response to present stress in cladocerans (Jansen et al., 2010; Suhett et al., 2011), it is still not clear how and for how long maternal effects persist over generations and in which circumstance they do. Thus, integrative studies combining epigenetic and life table approaches would greatly improve our understanding on the role played by epigenetic inheritance in stress resistance in a broader ecological and evolutionary scale. Again, cladocerans may be powerful models for such studies, due to the ease of performing multigenerational life table experiments with these organisms. Additionally, it can be easily tested with cladocerans how different degrees of offspring exposure inside the mother's body modulate maternal effects. Those degrees may range from no exposure (when the mother is exposed to a stressor before producing eggs) to the exposure of the offspring to the stressor as eggs or embryos inside the brood chamber.

5. Do Cladocerans Still Have Something to Contribute?

Studies with cladocerans have already generated lots of information, both in quantitative and in qualitative terms, about the way organisms react to stress. But they still can bring new insights to the research on stress in an ecological perspective and fill some pending gaps (Ebert, 2011; Miner et al., 2012).

One topic still overlooked in ecology is the influence of stress on biotic interactions, such as competition. This is a fundamental issue, because stress differentially changes the life history and competitive abilities of species, which certainly have impacts on their co-existence. For example, Santangelo et al. (2008) have shown that the abundance of *M. micrura* in a costal lagoon was positively related to salinity, whereas the opposite was found for other co-occuring microcurstaceans. Nevertheless, in laboratory life table experiments, salinity increases in the same range negatively impacted *M. micrura* fecundity, longevity and growth. The authors assumed that in the field, salt stress could have relaxed competition between *M. micrura* and other filter-feeding microcrustaceans, but no mechanistic test of this hypothesis was conducted. Recently, Bouchnak & Steinberg (2014) showed that increasing chemical stress by humic substances differentially affect the congeneric *M. macrocopa* and *M. micrura*: the latter had higher clutch size and did not reduce its reproductive output under poor-quality diets, being supposedly a better competitor. But competition was not directly tested in the experiments. Actually, only few studies test the effect of stress on competition using zooplankton (*e.g.,* Nandini & Sarma, 2002; Bernot et al., 2006). We still need studies properly designed to evaluate the effects of several environmental stressors on ecological interactions (Bengtsson, 1987). Additionally, there is evidence that even congeneric species may have contrasting responses to the same stressor (Steinberg et al., 2010b). This suggests that stress may have still underestimated roles in community assembly and persistence.

Understanding the consequences of stress is not a simple task, because stress outcomes for different response variable at different levels of biological organization may be even contradictory. Thus, more integrative studies are needed, which encompass stress responses at multiple levels of organization. We believe that cladocerans are particularly suitable organisms for this purpose, because of their short lifespan, which allows the appraisal of the overall output of stress at multiple life history traits simultaneously in life table experiments. This approach could be combined with "-omic" techniques such as microarrays for unraveling the molecular, biochemical and metabolic pathways governing the way by which organisms deal with stress. Additionally, direct investigations of epigenetic inheritance should be integrated with multigenerational experiments on life history traits and inducible morphological responses under stress for a better understanding of the stability and ecological relevance of epigenetic mechanisms for stress resistance and species evolution.

Although some authors argue that the pelagic habitat is rather stable in terms of chemical and physical properties (Lampert, 1997; Bijlsma & Loeschcke, 2005), this does not hold true, particularly in the tropics, for shallow ecosystems such as coastal lagoons (Caliman et al., 2010), and not under conditions forced by global climate change (Shurin et al., 2010). In a shallow ponds and coastal lagoons, water temperature, for instance, may vary by almost 8 °C during 24h, which certainly exert thermal stress on planktonic organisms (Khan et al., 1970; Guiral et al., 1994; Kjerfve & Knoppers, 1999). Comparable thermal amplitudes are also experienced by zooplankton in deeper ecosystems when these organisms undergo a diel vertical migration forced by environmental factors such as predation, and it may induce thermal stress (Mikulski et al., 2011). The effects of increasing and decreasing mean temperature on cladocerans life history have been vastly studied, but the effects of the amplitude of diurnal temperature variation have been mostly overlooked (but see Chen & Stillman, 2012). Nevertheless, that is the real situation organisms have to face in nature, as is the case of the environments mentioned above. Shallow coastal lagoons represent an interesting environmental context for these questions, because predictions of future climatic changes suggest that these ecosystems will experience more frequent sand-bar opening and salt intrusion from the ocean, which means a shallower, more thermally-fluctuating water column, and higher mean salinities over time (Anthony et al., 2009; Marengo et al., 2010). Again, cladocerans can be successfully used as model organisms for laboratory studies using incubation devices which allow oscillating temperature regimes.

Finally, the peculiarity of clones in stress response still needs to be better integrated into a populational perspective. Since each clone may respond in a particular way to a stressor, the outcome of stress at the population level will be a balance of the outcomes of the clones present. Thus, data on genetic structure of natural populations must be combined with clone-specific experiments for modeling the overall stress effects on the population life history traits and their consequences for communities and ecosystems.

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