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Review article

Active and passive spatial avoidance by aquatic organisms from environmental stressors: A complementary perspective and a critical review

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ABSTRACT

Spatial avoidance is a mechanism by which many organisms prevent their exposure to environmental stressors, namely chemical contaminants. Numerous studies on active avoidance and drift by aquatic organisms, as well as the main approaches used to measure both responses, were reviewed. We put forward a particular recommendation regarding methodological approaches: active avoidance should preferably be evaluated under a dilution gradient in a multi-compartmented system instead of in a bi-compartmented system. Available data on spatial avoidance from contamination indicate that emigration can occur at even lower contaminant concentrations than sub-individual noxious effects (assessed with the traditional forced-exposure assays), challenging the widely accepted paradigm in ecotoxicology that contaminant-driven adverse consequences at the population level result from a time delayed cascade of sequentially linked biochemical, cellular, physiological, and finally whole organism deleterious effects. Therefore, contaminants should not be viewed solely as potential toxicants at the individual level, but also as potential disturbers of habitats, by making the latter, at least partially, unsuited to accommodate life. Also, exposure to contamination is needed to trigger avoidance, but uptake is not mandatory, which demands the concept of exposure to be expanded, to include also the mere perception of the stressor. Since emigration eventually leads to local population extinction, and thus to severe implications for ecosystem structure and functioning, we then recommend that avoidance data be incorporated in environmental risk assessment schemes.

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1. Introduction

Traditionally, in environmental stress ecology, to determine concentration-response relationships, organisms are forcedly exposed to a stressor (e.g. abiotic variable, pure chemical or natural sample) and a specific biological response is measured in each tested concentration. However, forced exposure lacks ecological relevance by wrongly considering organisms as exclusive passive uptakers (Lefcort et al., 2004). According to Willmer et al. (2000), under changing environmental conditions organisms can present conformity, regulation or avoidance. Since the first two responses imply direct (internal repair mechanisms) and indirect (changes in fitness and in the interactions with the environment) additional energy costs, the decision of escaping to reduce the exposure to stressors tends to be beneficial (De Lange

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et al., 2006). Therefore, forced-exposure approaches can be unrealistic for organisms that recognizably can detect environmental stress and escape from it. Remarkably, although being frequent in nature, both spatial (displacement towards other areas by swimming, flying, walking, or drifting) and temporal (dormant stages and postponing colonisation of unsuited habitats, e.g. a midge not settling in a contaminated sediment or a dragonfly not ovipositing eggs in a contaminated pond) avoidance have received much less attention in environmental stress ecology than other individual sub-lethal responses.

When spatial avoidance is considered, an important distinction should be made between active and passive avoidance. Active spatial avoidance from environmental stressors results from the ability either to detect a chemical and to move (by swimming, flying, walking) towards less stressed environments or to change the behavior (e.g. unburrowing) (Roper and Hickey, 1994; De Lange et al., 2006; Hellou, 2011; Ward et al., 2013). As for passive avoidance or drift, it occurs when air or water flow is responsible for the organisms' displacement (Humphries and Ruxton, 2003; Hogan and Mora, 2005). The ecological consequences of avoidance can be as severe as mortality or reproduction impairment, since it can locally lead to population extinction (Lopes et al., 2004). Furthermore, because organisms' evasion from contaminants may occur before lethal and, even, sub-lethal physiological effects take place, and thus at the lowest levels of stress capable of eliciting an adverse environmental effect, under such circumstances the ecological risk of a stressor might increase (Fleeger et al., 2003; Aldaya et al., 2006; Rosa et al., 2008).

A widely accepted paradigm in ecotoxicology is that contaminant-driven adverse consequences at the population level result from a time delayed cascade of sequentially linked biochemical, cellular, physiological, and finally whole organism noxious effects (Newman and Unger, 2001; Walker et al., 2001). Avoidance is a response that demands an additional complementary perspective since it may occur involving neither the uptake of contaminants, nor sub-individual noxious effects. Therefore, contaminants should not be viewed solely as potential toxicants at the individual level, but also as potential disturbers of habitats, by making the latter, at least partially, unsuited to accommodate life. Also, exposure to contamination is needed to trigger avoidance, but uptake is not mandatory, which demands the concept of exposure to be expanded, to include also the mere perception of the stressor. Therefore, to quantify exposure looking solely at uptake can lead to a serious underestimation of the ecological risk. As an example, when the avoidance response of the amphipod *Corophium volutator* exposed to polycyclic aromatic hydrocarbon (PAH)-spiked sediment was triggered, the levels of PAH accumulated in the organisms were a thousand times lower than those associated to narcosis (Hellou et al., 2008).

According to several authors (Swartz et al., 1982; Smith and Bailey, 1990; Åtland and Barlaup, 1995; Hansen et al., 1999; Svecevičius, 2001; Aldaya et al., 2006; Hellou, 2011), integrating avoidance in ecotoxicological studies can also give an indication on the populations' spatial distribution and community diversity in contaminated habitats as well as in neighbour uncontaminated areas. Hansen et al. (1999) showed that the population abundance and distribution of the rainbow trout, *Oncorhynchus mykiis*, in areas contaminated with metals and acidity, could be partially explained by the escape of organisms to avoid contamination; the latter represents, thus, a threat as a habitat disturber, due not only to direct effects on organisms, but also indirect effects by triggering emigration. Similarly, the distribution of local amphipods and chironomids was inversely associated to the sediment toxicity levels that indicated a contaminant-driven spatial arrangement (Swartz et al., 1982; Hare and Shooner, 1995). Besides field observations, many studies have been performed using different organisms and contaminants to assess the ability of organisms to avoid contaminants as well as to estimate the concentrations that trigger avoidance.

The present review intended (i) to summarize the available knowledge on active spatial avoidance and drift by aquatic organisms triggered by the presence of stressors, mainly contaminants; (ii) to discuss the role of contaminants as toxicants at the individual level versus as habitat disturbers; and (iii) to evaluate the importance, at the ecosystem level, of spatial avoidance from stress and the possible future inclusion of avoidance testing in ecological risk assessment (ERA) schemes for aquatic ecosystems. Although avoidance tests have been widely exploited in preliminary soil quality assessment schemes and a procedure for an avoidance test has already been standardized (International Organization for Standardization 17512; ISO, 2008), our focus in the present review was on aquatic ecosystems, because avoidance has received little attention in ERA for the aquatic compartment.

2. Active avoidance by water-column organisms

The traditional use of forced exposure in bioassays can be justified based on many reasons, being the following three among the major ones: they are easy-to-use, allow the establishment of an unequivocal concentration-effect relationship at the individual level, and offer readily interpretable results. However, if the prime ecological effects of stressors to be measured are those occurring at community and ecosystem levels, individual effects measured under forced exposure might limit the evaluation of environmental risks (Amiard-Triquet, 2009). Different approaches based on assessing avoidance responses have intended to solve this problem. The first experiments on spatial avoidance by aquatic organisms were performed with fish and aimed to simulate a stressor gradient within a tube by injecting clean water and a contaminant in the opposite extremities (Jones, 1947, 1948). Further designs with two compartments (Folmar, 1976; Gunn and Noakes, 1986; Svecevičius, 1999), steep-gradients, laminar flow chambers (Hartwell et al., 1989), avoidance/preference chambers (Smith and Bailey, 1990), and fluvarium systems (Richardson et al., 2001) have also been employed; in the eighties a summary of the main methods used over the last few decades to assess avoidance from contaminants by fish was made by Rand (1984).

All above-mentioned approaches to measure spatial avoidance present a similar characteristic: the use of a bi-compartmented system. As stated by Jones (1947), the use of a system with two distinct areas in which a sharp difference in the contaminant concentration is established allows fish to discriminate between two clearly defined environments. Such an approach makes sense but only when under a real field situation a contamination gradient is not expected, and, therefore, two distinct areas with a sharp difference in the contaminant concentration are formed. In addition, by using this approach, the experimental outcomes are restricted to the calculation of the avoidance percentage for a given concentration, preventing a wider understanding on the ecological consequences of the avoidance response. The contamination in aquatic systems generally disperses as a dilution gradient, with stress being negatively correlated with the distance from the contamination source. Consequently, toxicity assays whose organisms are exposed under confined conditions with no possibility to escape or, even, in bi-compartmented systems, are often an unrealistic simulation of exposure. Therefore, to better simulate real contamination scenarios, active avoidance should preferably be evaluated under a dilution gradient (Moreira-Santos et al., 2008; Rosa et al., 2008, 2012), where all different contamination levels are accessible to the exposed organisms. By establishing a linear contamination gradient across different concentrations along the exposure system, it is possible to best predict the spatial distribution of the population when exposed to a similar gradient under a real scenario of contamination. Furthermore, results from an assay in a system with a contamination gradient may be directly used to compute median avoidance concentrations (AC50), i.e., the concentration eliciting avoidance by 50% of the organisms (Moreira-Santos et al., 2008).

Studies to evaluate active spatial avoidance with aquatic organisms in response to habitat disturbance (i.e., natural or spiked waters with a wide range of contaminants) are summarised by biological group in Table 1 and some relevant results are briefly described here. Active