Stressor-driven emigration and recolonisation patterns in disturbed habitats

Cristiano V.M. Araújo [a,b,*], Matilde Moreira-Santos [a], Rui Ribeiro [a]

[a] CFE – Centre for Functional Ecology, Department of Life Sciences, University of Coimbra, Calçada Martim de Freitas, 3000-456 Coimbra, Portugal
[b] Institute of Marine Sciences of Andalusia (CSIC), Department of Ecology and Coastal Management, 11510 Puerto Real, Spain

HIGHLIGHTS

- Zebrafish avoidance (Av) and recolonization (Rc) responses were assessed.
- Fish were non-forcedly exposed along an acid mine drainage (AMD) gradient.
- AC_{50} values of AMD for fish were not statistically different in 3-m or 30-m systems.
- Emigration is distance-independent but time-correlated (spacelessness hypothesis).
- Av and Rc responses were inversely proportional ($AC_x = RC_{100-x}$) (Av-Rc hypothesis).

GRAPHICAL ABSTRACT
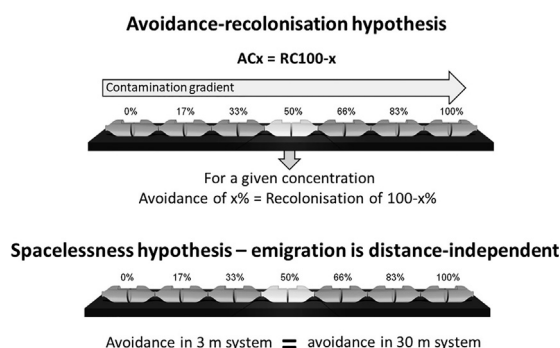
ARTICLE INFO

ABSTRACT

Although essential to conservation, little is known about how stress intensity can provoke emigration from disturbed habitats and allow recolonisation of those same environments. To demonstrate the applicability of laboratory experiments, we tested two hypotheses empirically using zebrafish response to artificially polluted environments that exhibited a linear gradient of stressor (acid mine drainage) levels. We hypothesized that emigration is distance-independent but time-correlated (spacelessness hypothesis). Additionally, we hypothesized that stressor-driven emigration could predict the extent of population growth in recovering habitats (avoidance-recolonisation hypothesis). For example, if half the organisms emigrate at a given stressor level, then the remainder should be able to recolonise a habitat experiencing the same stressor intensity. Comparisons of the small-scale experiment with a larger-scale simulation suggested that controlled laboratory results can be extrapolated to field populations (although time to perceive the contamination gradient may pose differential individual effects) because AC_{50} (median avoidance concentration) values of an acid mine drainage sample (AMD) were not statistically different when fish were exposed to the same gradient in 3-m long [0.50% (0.43–0.57)] or 30-m long [0.73% (0.30–2.2)] systems. Regarding the avoidance-recolonisation hypothesis, the number of recolonisers was inversely proportional to the number of avoiders ($AC_x = RC_{100-x}$). In particular, the similar distribution of fish along the 0–3% AMD gradient in both avoidance and recolonisation experiments resulted in identical AC_{50} and RC_{50} values: 0.55% (0.34–0.87) and 0.55% (0.45–0.67) AMD, respectively. The inclusion of avoidance and recolonisation responses in the environmental risk assessments provides a novel perspective of risk based on the emigration of organisms and contributes to the understanding and prediction of biological invasions and ecosystem recovery after restoration.

© 2018 Elsevier B.V. All rights reserved.

* Corresponding author at: Institute of Marine Sciences of Andalusia (CSIC), Department of Ecology and Coastal Management, 11510 Puerto Real, Spain.
E-mail addresses: cristiano.araujo@icman.csic.es, (C.V.M. Araújo), matilde.santos@zoo.uc.pt, (M. Moreira-Santos), rui.ribeiro@zoo.uc.pt (R. Ribeiro).

1. Introduction

The niche theory predicts that populations will eventually experience extinction when an environmental condition changes and falls outside the range within which organisms are able to reproduce (Van Straalen, 2003; Begon et al., 2006). However, a much lesser change, leaving the habitat still well within that range, could also dictate population extinction if organisms emigrate to adjacent un- or less disturbed habitats. For example, dilutions of several pulp mill effluents eliciting active spatial avoidance by 50% of 12-h long exposed organisms (the cladoceran *Daphnia magna*) were similar to those reducing reproduction by 50% after a 42-fold longer forced exposure (21 d) (Rosa et al., 2010). In other words, if a less disturbed habitat was available, the organisms would have moved away before they began suffering adverse physiological effects.

Organisms can respond to a stressor with either 'fight or flight' (Hobfoll, 1988). Avoidance is considered the 'flight' option, and can be temporal or spatial. The former includes catatonic, 'playing dead' behaviours and physiological life-history events (e.g. torpid and dormant stages, cryptobiosis), while the latter can be split into passive (drift) or active (i.e. self-propelled) avoidance (Hobfoll, 1988; Liess, 1994; Willmer et al., 2005; Araújo et al., 2016a).

The acceptance of a niche-based concept of stress neglects the ecological consequences of the "flight" option at higher (than the individual) levels of biological organization. For example, Steinberg (2012) put forward that stress is a physiological state in an organism placed outside its niche. In our view, a more valuable perspective of stress is one that accounts for levels of biological organization beyond the individual. Parker et al. (1999) proposed a definition of stress that involves stressor-induced negative impact, not just on individuals, but any biological unit (e.g. population, community). This expanded concept of stress, which was also sanctioned by van Straalen (2003), accommodates the framework of the chemical stress ecology (sensu Van den Brink, 2013) and aligns with the idea of stressors (e.g. environmental pollution) that extend beyond the individual level to affect habitats, decreasing their suitability for accommodating life (Beketov and Liess, 2012; Moe et al., 2013). For our purpose, habitat disturbance is an event that alters resources or any aspect of the abiotic environment, thereby structurally and functionally disrupting populations, communities, or ecosystems (Molles, 2015). Conservation efforts in response to such disturbance will greatly benefit from data on avoidance behaviour especially in species with small populations, as such groups are more vulnerable (Begon et al., 2006; Moe et al., 2013). Available data on some anurans (Araújo et al., 2016a) demonstrate their ability to actively emigrate from stressors. Furthermore, genetic erosion and other multigenerational effects are expected in a population if avoidance behaviour is genetically determined (Lopes et al., 2004), meaning that the most sensitive genotypes emigrate first (Ribeiro and Lopes, 2013).

Small-scale experiments have been performed to obtain insight on avoidance behaviour (Araújo et al., 2016a). Such experiments are practical and allow high replicability (Schindler, 1998; Bergström and Englund, 2004; Petersen and Englund, 2005; Greathouse et al., 2006; Vignati et al., 2007; Englund and Leonardsson, 2008), but considerable uncertainty may exist in attempting spatial extrapolations of laboratory experimental data to field conditions. However, here we suggest that active avoidance intensity is spaceless—independent of distance—but affected by time, specifically the duration between exposure to the negative stimulus and its detection, as well as the time required per species for dispersal. This 'avoidance spacelessness hypothesis' is based on the assumption that the proportion of potential escapers within a population is constant (i.e., avoidance percentage is dependent on the concentration regardless the distance). Consequently, the final spatial distribution along a stressor gradient will be constant, though the time necessary to achieve that distribution is positively correlated to distance. Thus, given enough time, final spatial distributions along similar stressor gradients with differing spatial scales will match. At any given

moment, a lowest effective gradient may exist (the smoothest gradient organisms can detect and avoid; Moreira-Santos et al., 2008), but over time, its value (in concentration per distance units) will asymptotically converge to zero. This hypothesis has three assumptions: absences of (i) toxicological effects, (ii) acclimation phenomena, and (iii) spatial-distribution distortions from density-dependent effects or other (a) biotic interference. If validated, this hypothesis allows for increased accuracy in extrapolating results on the intensity of stressor-induced habitat disturbance from small-scale experiments on stressor-driven emigration to the field.

Understanding avoidance responses may provide insight into the extent of population regrowth in recovering habitats, an aspect that has received little attention (Van den Brink, 2008), although being crucial for the ecological risk assessments involved in endangered-species conservation and the management of protected areas. The notion and concept of emigration followed by recolonisation after a habitat change dates back to as far as the XIXth century, with Charles Darwin (Darwin, 1859): "The arctic forms, during their long southern migration [in the Glacial period] and re-migration northward, will have been exposed to nearly the same climate". Here, we developed the avoidance-recolonisation hypothesis, which postulates that intensities of the two responses are inversely correlated. An emptying habitat (from stressor-driven emigration) will be recolonised by adjacent populations upon sufficient reduction of stressor intensity to partially unavoided levels. Within any population, if the proportion of escapers in a future habitat disturbance is *x*% then the proportion of recolonisers of an adjacent habitat with the same level of stress will be 100-*x*%. In other words, the stressor intensity causing *x*% avoidance will allow a 100-*x*% recolonisation. The hypothesis has two assumptions. The first is identical to the third assumption (on spatial-distribution distortions) of the avoidance spacelessness hypothesis. Second, the speed and the number of escapers and recolonisers should be equally affected by the pattern of previous exposure they were faced with, along the stressor gradient, in their respective scenarios. For instance, if a stressor is partially narcotic, then recolonisation will be more intense than avoidance (emigration), whereas the opposite should be true for a stimulant drug. Also, acclimation (sensu Willmer et al., 2005) may result in decreased avoidance intensity compared with recolonisation intensity.

A complete model of stressor effects would take into account exposure, stressor level (e.g. pollutant toxicity), species movement, and life cycles (Liess and von der Ohe, 2005). Our two proposed hypotheses are tools that can address species movement patterns and integrate population recovery into the evaluation of stressor effects, addressing the current deficit in the literature (Van den Brink, 2008). In terms of species movement, we note that traditional evaluations of stressor effects implemented inescapable exposure, thus entirely neglecting the possibility of active emigration (Liess and von der Ohe, 2005; Knillmann et al., 2018). Yet, our understanding of stressor effects is incomplete without taking into account escapers and invaders, as well as organisms that remain (conformers and regulators) (Moe et al., 2013). The forced-exposure conditions of laboratory or semi-field experiments, lacking connectivity to undisturbed habitats, could result in underestimation of population recovery, through recolonisation (Van den Brink, 2008), but could also result in underestimation of adverse effects during exposure, through emigration (Lopes et al., 2004).

In the present study, we aimed to link both exposure (emigration/escape) and post-exposure (subsequent immigration/recolonisation) effects through experiments that tested both the avoidance spacelessness and the avoidance-recolonisation hypothesis. Zebrafish (*Danio rerio*) was selected as subjects because of their mobility, size, and ability to avoid stressors (Moreira-Santos et al., 2008; Araújo et al., 2014a). Our study should contribute to the prediction of recolonisation (immigration) rates using experimental data on stressor-driven emigration.