When Complexity Rimes with Sanity: Loss of Fractal and Multifractal Behavioural Complexity as an Indicator of Sublethal Contaminations in Zooplankton

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Abstract

Natural and anthropogenic sources of contamination such as plankton toxins and hydrocarbons are nearly ubiquitous in the marine environment. Specifically, they are a pernicious threat especially at low concentration as nonlethal effects on the plankton propagate through the food chain and accumulate in the tissues of top predators, ultimately putting human health at risk. In this contribution, I first describe how the complexity observed in the spatial and temporal patterns of copepod swimming behaviour can be objectively quantified using a series of 'behavioural stress indexes' based on fractal and multifractal analyses of copepod swimming behaviour and swimming sequences. These indexes are suggested as a potential tool to critically assess behavioural responses to natural and anthropogenic forcing in the marine environment.

1   Introduction

As observed across the whole spectrum of social and natural sciences, behavioural data are inherently very complex (Seuront 2010a, b), a priori lacking of any spatial pattern or temporal structure (Fig. 1). This complexity is believed to be biologically adaptive as it avoids restricting the functional response of an organism to highly periodic behaviour (Goldberger et al. 2000) and it is error tolerant, allowing organisms to cope with stress and unpredictable environments (Goldberger et al. 1990). The analysis of behaviour hence critically requires approaches explicitly dealing with this complexity. This issue is particularly relevant in welfare assessment as most behavioural measures are not sensitive enough to detect subtle changes associated with mild or acute stress (Rutherford et al. 2004).

The field of behavioural ecology has recently begun to use novel analytical tools such as fractal analysis (Asher et al. 2009). Specifically, fractal

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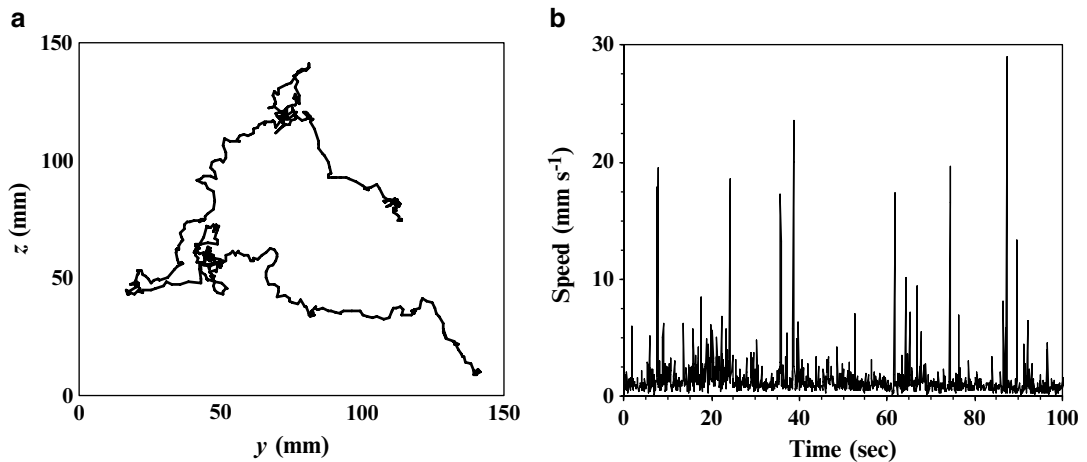UMR 8187 LOG, Wimereux, France
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Fig. 1 Illustration of the intrinsic complexity perceptible in the spatial pattern (**a**) and temporal structure (**b**) of zooplankton swimming behaviour. (**a**) Two-dimensional projection of the three-dimensional trajectory of an adult male *Eurytemora affinis*. (**b**) Time series of the instantaneous speed of an adult *Temora longicornis* female. Both behaviours were recorded at 25 frames s^{-1} in a cubic ($15 \times 15 \times 15$ cm) glass chamber from *E. affinis* and *T. longicornis* individuals swimming freely in filtered estuarine and coastal waters, respectively

analysis has been introduced in the study of human physiology to distinguish between systems operating in normal vs. pathological states (Ivanov et al. 1999; Mishima et al. 1999). Both the temporal and structural complexity of a range of biological systems hence decrease under stressful conditions. For instance, the time series of beat intervals in healthy subjects have more complex fluctuations than patients with severe cardiac disease (Ivanov et al. 1999). Similarly, the geometry of the lung terminal airspace branching architecture is more complex in normal subjects than in patients with chronic obstructive pulmonary disease (Mishima et al. 1999). More specifically, stressed (e.g. diseased and parasited) animals typically reduce the complexity of their behavioural display (Alados et al. 1996). Fractal analysis has hence been extensively used as a non-invasive assessment of the general health of wild and captive animals (Rutherford et al. 2004; Alados et al. 1996), including copepods (Seuront 2011).

The quantitative assessment of changes in copepod swimming behaviour is critical as swimming and feeding are intertwined in most copepod species, hence any disruption of copepod swimming is predicted to have detrimental consequences to their biology and ecology (Seuront 2012), which in turn may affect ecosystem structure and function and geochemical fluxes. Behavioural changes have the potential to be used as indicators of ecosystem health. This issue is particularly relevant for sublethal toxicant concentration as behavioural changes provide sensitive non-invasive sublethal endpoint with short-response time for toxicity bioassays, which are more sensitive than mortality responses (Garaventa et al. 2010).

Over the last two decades, fractal analysis has increasingly been used to describe and provide further understanding to zooplankton swimming behaviour. This may be related to the fact that fractal analysis has the desirable properties to be independent of measurement scale and to be very sensitive to even subtle behavioural changes that may be undetectable to other behavioural variables (Rutherford et al. 2004; Coughlin et al. 1992). As early claimed (Coughlin et al. 1992), this creates 'the need for fractal analysis' in zooplankton behavioural ecology in general and in zooplankton ecotoxicology in particular.

In this context, I first briefly rehearse the very basic principles of fractal theory before describing a few fractally derived 'behavioural stress indexes'

that can be directly applied to various aspects of zooplankton behavioural complexity and used to infer the stress experienced by these organisms under a range of conditions. I subsequently introduce the more elaborated and still seldom used, though more general, concept of multifractal that may conveniently be used as an objective and quantitative tool to thoroughly identify models of movement behaviour, such as Brownian motion, fractional Brownian motion, ballistic motion, Lévy flight/walk and multifractal random walk. I stress that fractal and multifractal analyses can detect differences in behavioural complexity, where traditional measures cannot. As such, I finally discuss their relevance as a practical tool to infer the nature of both natural and anthropogenic forcing.

2　From Fractal Theory to Stress Assessment: Behavioural Stress Indexes

2.1　A Few Words on Fractals

A fractal is 'a rough or fragmented geometric shape that can be split into parts, each of which is (at least approximately) a reduced-size copy of the whole' (13). This property is called *scale invariance* and means that the observed structure remains unchanged under magnification or contraction. This scale invariance can be observed in two distinct, though conceptually similar, forms referred to as *self-similarity* and *self-affinity*.

Self-similarity has traditionally been illustrated using theoretical fractal objects (Mandelbrot 1982). A more realistic construction of a fractal object, a fractal tree, is shown in Fig. 2. In contrast, self-affinity characterises an object that may be written as a union of rescaled copies of itself, where the rescaling is anisotropic, that is, dependent on the direction. A typical example of self-affinity is given by the temporal patterns of the successive speed of copepods (Fig. 1b); it looks rough, like their trajectory (Fig. 1a), but with the two axes corresponding to physical quantities that are fundamentally different.

A fundamental consequence of scale invariance is, as originally described for the length of the coast of Britain (Mandelbrot 1982), that the length of, for example, copepod trajectories (Fig. 1a) does not converge towards a fixed value, but keeps increasing, *theoretically* without any upper limit, but see Rutherford et al. (2004) for a detailed discussion on the topic. As a consequence, in contrast to Euclidean lines, they cannot be differentiated or integrated, hence cannot be described by an integer dimension. The complexity of scale invariant patterns and processes can, however, be described by a dimension D, the so-called fractal dimension. In contrast to Euclidean dimensions, a fractal dimension is fractional. For instance, the Euclidean dimensions, d, of a line, a circle and a cube are, respectively, 1, 2 and 3. The trajectory of a copepod has, in turn, a fractal dimension, D, bounded between $D=1$ when the copepod swims along a completely linear path and $D=2$ when the movements
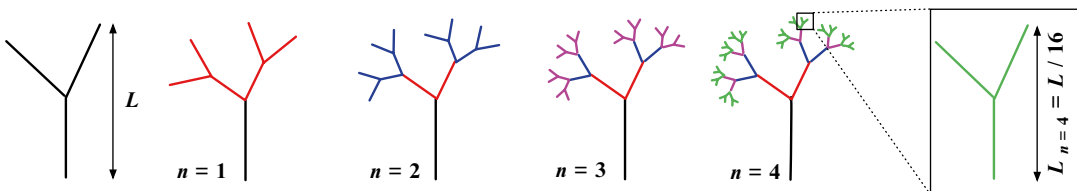

Fig. 2 Illustration of the first four successive steps of the iterative process leading to a self-similar fractal tree. At each step n of the process, each terminal branch of the tree is replaced by a rescaled version of the original tree. Here the scale ratio between two successive steps is 2, i.e. at a step n, each branch is replaced by a tree, which is a copy of the original tree reduced 2^n times. Hence, when $n=4$, the resulting ramifications are 2^4 times smaller than the original tree

are so complex that the trajectory fills the whole available space. The fractal dimensions reported in the literature for zooplankton trajectories (essentially cladocerans and copepods) typically fall in the range 1.0–1.8, indicating a range of behavioural strategies that may be related to the nature of the physical, chemical and biological cues present in the water (Rutherford et al. 2004; Seuront 2012, 2013; Garaventa et al. 2010; Shimizu et al. 2002).

Three types of behavioural data can be used in fractal analysis: (1) two- or three-dimensional movement pathways, (2) the temporal patterns of successive displacements (or equivalently speed) and (3) observation of the presence or absence of a behavioural state scored on a binary scale, i.e. whether an animal is active or inactive, or fluctuations between two behavioural states. In the next section, I provide a set of fractal techniques to analyse these behavioural data and briefly review how they were used to assess the stress experienced by zooplanktonic organisms.

2.2 Fractals as a Stress Assessment Tool in Zooplankton Behavioural Ecology

2.2.1 The Fractal Nature of Copepod Spatial Patterns

I describe hereafter three conceptually similar methods—the box-counting, the dividers and the mass dimension methods—that can be easily implemented to quantify the geometric complexity of copepod trajectories (Rutherford et al. 2004). Note that whilst these methods are discussed in the general framework of three-dimensional trajectories, they can be equivalently implemented in two dimensions.

The box-counting method relies on the δ cover of a trajectory, i.e. the number of boxes of length δ required to cover the trajectory. Practically, this procedure consists in superimposing a regular grid of boxes of length δ on the trajectory and counting the number of boxes that intersect the

trajectory. This procedure is repeated using different values of δ. The volume occupied by a trajectory is then estimated using a series of boxes spanning a range of volumes down to some small fraction of the entire volume. The number of occupied boxes increases with decreasing box size, leading to the following power-law relationship:

$$N(\delta) \propto \delta^{-D_b} \qquad (1)$$

where δ is the box size, $N(\delta)$ is the number of boxes intersecting the trajectory and D_b is the box fractal dimension; D_b is estimated from the slope of the linear trend of the log-log plot of $N(\delta)$ vs. δ.

The divider dimension D_d (also referred to as the compass dimension) is estimated by measuring the length of a trajectory at various scales δ. The procedure is analogous to moving a set of dividers (like a drawing compass) of fixed length δ along the trajectory. The estimated length of a trajectory $L(\delta)$ increases with decreasing δ as $L(\delta) \propto \delta^{1-D_d}$. As the estimated length $L(\delta)$ is also the product of $N(\delta)$ (the number of compass dividers required to cover the trajectory) and δ (i.e. $L(\delta) = N(\delta)\delta$), this can equivalently be written as

$$N(\delta) \propto \delta^{-D_d} \qquad (2)$$

The divider dimension D_d is then estimated from the slope of the linear trend of the log-log plot of $N(\delta)$ vs. δ.

The mass dimension method counts the number of pixels occupied by a trajectory in sampling cubes ($\delta \times \delta \times \delta$). The mass $m(\delta)$ of occupied pixels is subsequently defined as $m(\delta) = N_O(\delta)/N_T(\delta)$, where $N_O(\delta)$ and $N_T(\delta)$ are, respectively, the number of occupied pixels and the total number of pixels within an observation window of size δ. These computations are repeated for various values of δ, and the mass dimension D_m is defined as

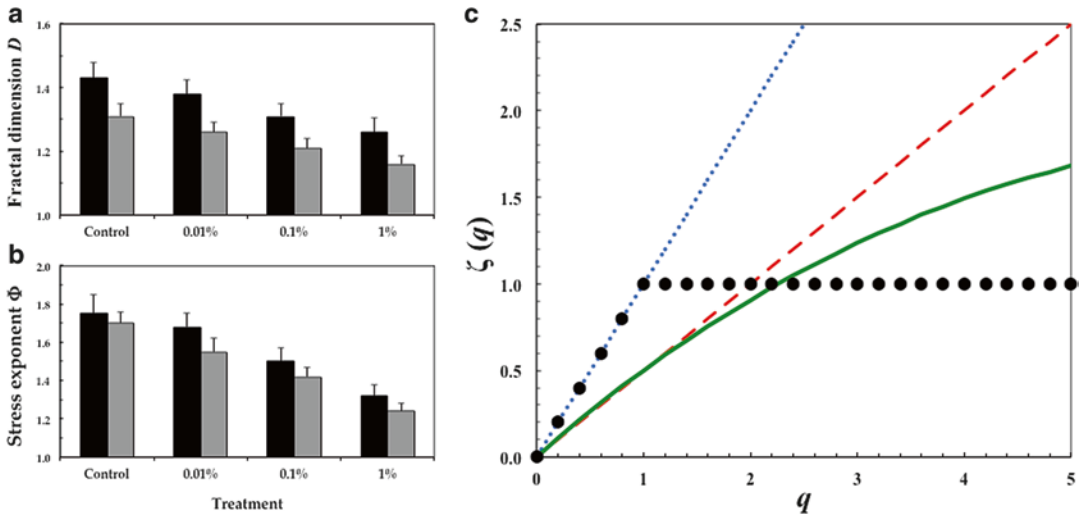$$m(\delta) \propto \delta^{D_m} \qquad (3)$$

Fig. 3 The fractal dimension D (**a**) and stress index ϕ (**b**) estimated from the swimming behaviour of *Eurytemora affinis* adult males (*black*) and non-ovigerous females (*grey*) in control uncontaminated estuarine water and in estuarine water contaminated with the water-soluble fraction of diesel oil at 0.01, 0.1 and 1 % (Modified from Seuront 2010a, b). (**c**) The multifractal function $\zeta(q)$ allows to identify a range of movement behaviour (see text for details) such as ballistic motion (*dotted blue line*), Brownian motion (*red dashed line*), optimal Lévy flight (*black dots*) and multifractal random walk (*continuous green curve*) (Modified from Seuront and Stanley 2014)

where the fractal dimension D_m is estimated from the slope of the linear trend of the log-log plot of $m(\delta)$ vs. δ.[1]

The results of studies based on a geometric assessment of zooplankton behavioural complexity under various conditions of water contaminations—i.e. short-term exposure to copper, organophosphorus and carbamate (Shimizu et al. 2002), the water-soluble fraction of diesel oil (Seuront 2010a, b, 2012), nonylphenol, cadmium and a mixture of polycyclic aromatic hydrocarbons (Michalec et al. 2013a, b)—lead a variety of a priori conflicting conclusions, including no change (Michalec et al. 2013a, b), a decrease (Seuront 2010a, b, 2012; Fig. 3a) and an increase (Seuront 2010a, b) in the geometric complexity of swimming behaviour.

2.2.2 The Fractal Nature of Copepod Temporal Patterns

One of the most extensively used techniques to detect temporal self-affine patterns is power spectral analysis. Formally, a power spectrum is defined as the square of the amplitude of the Fourier transform of a time series of a descriptor; it is hence an expression of the variance of the descriptor at different temporal scales. In practice, the power spectral density $E(f)$ is given by $E(f) \propto f^{-\beta}$, where f is the frequency (s^{-1}; $f = 1/t$, where t is time). The spectral exponent β is estimated as the slope of a log-log plot of $E(f)$ vs. f. Specifically, the value of the exponent β provides an efficient way to classify the type of motion behaviour exhibited by zooplankton organisms.[2]

Spectral analysis has still barely been used in zooplankton behavioural ecology (Uttieri et al. 2008; Dur et al. 2010) but nevertheless suggests

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[1] Note that it is readily seen from Eqs. (1) and (2) that $D_b = D_d$, whilst more convoluted developments show that $D_b = D_m$; hence $D_b = D_d = D_m$; see (Seuront 2010a) for details. Statistically inferring the absence of significant differences between fractal dimensions returned by different methods of analysis hence constitutes an additional guarantee of the trustworthiness of the fractal dimension estimates.

[2] Brownian motion (i.e. normal diffusion) is characterised by $\beta = 2$. Anti-persistent and persistent fractional Brownian motions are characterised by $\beta < 2$ and $\beta > 2$, respectively. Specifically, a motion is persistent in the sense that an organism moving in some direction at time t will tend to move in the same direction at the next time step.

that zooplankton organisms exhibit a range of behaviour including fractional Gaussian motion, fractional Gaussian noise and pure random noise.[3]

2.2.3 The Fractal Nature of Behavioural States

Self-affine techniques based on the analysis of frequency distributions of behavioural states were used to infer the response of zooplankton to a range of stressors. They include considerations of the scaling properties of the probability distribution functions (PDFs) of either the time tx spent in a specific behavioural state x (i.e. $p(t_x) \propto t_x^{-c}$) (Schmitt et al. 2006) or the velocity v_x used to define different behavioural states x (i.e. $p(v_x) \propto v_x^{-c}$) (Michalec et al. 2010). A few studies investigated the scaling properties of the cumulative probability distribution functions (CDFs) of move duration greater than a determined duration t ($P(t \leq T) \propto t^{-\phi_1}$) (Seuront and Leterme 2007) and move lengths L greater than a determined length l ($N(l \leq L) \propto l^{-\phi_2}$) (Seuront 2010a, b, 2011). These studies consistently found a decrease in the exponents ϕ_1 and ϕ_2, hence in behavioural complexity, for a range of copepod species exposed to sublethal concentrations of naphthalene (Seuront and Leterme 2007) and the water-soluble fraction of diesel oil (Seuront 2010a, b; Fig. 3b). In contrast, the exponent c was shown to increase in *Eurytemora affinis* following a short-term exposure to sublethal concentrations of nonylphenols (Michalec et al. 2013a, b).

Note that the behaviour of an organism alternating between two behavioural states can also be assessed through the construction of a binary sequence $z_t(i)$ for each behavioural activity taken from continuous observations. When a specific activity is observed, $z_t(i) = 1$, and $z_t(i) = 0$ otherwise. The resulting time series of binary sequences can further be integrated as $w_i(t) = \sum_{i=1}^{N} z_t(i)$, where N is the number of behavioural observations. The temporal pattern of the integrated variable $w_i(t)$ can then be analysed with self-affine techniques such as spectral analysis.

3 From Fractals to Multifractals: A Step Further in Zooplankton Stress Assessment

3.1 From Fractals to Multifractals

A measure (i.e. a physical quantity such as mass, energy, a number of individuals or more specifically the distance displaced by a copepod; Fig. 1b) has to be distinguished from its geometric support, which might or might not have a fractal geometry (Rutherford et al. 2004). Then, if a measure has different fractal dimensions on different parts of the support, the measure is a multifractal. Multifractals are hence a generalisation of fractal geometry initially introduced to describe the relationship between a given quantity and the scale at which it is measured. Whilst fractal geometry describes the complexity of a given pattern with the help of only one parameter (the fractal dimension), multifractals characterise its detailed variability by an eventually infinite number of sets, each with its own fractal dimensions.

An intuitive interpretation of multifractals is based on the spatial structure of modern cities (Rutherford et al. 2004). Consider a city viewed strictly from above, it can be considered as a succession of built (buildings) and unbuilt (streets and parks) areas. The only available information is hence the distribution of the built and the unbuilt areas. This is the geometric support of the city. Now, change the angle of vision by taking a position not directly above the city, but from the side. The city initially made of built and unbuilt areas is now a set of buildings with different heights. This is the measure we are now interested in. It is now possible to estimate the distribution of a wide range of building heights. Each height will (eventually) be characterised by a fractal dimension, hence the concept of multifractals.

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[3] For instance, the velocity components of *Clausocalanus furcatus* were both characterised by $\beta \approx 0$ (Uttieri et al. 2008), indicative of a random process without internal serial correlation. In contrast, β ranged from 0.30 to 0.75 in *Temora longicornis* (Moison et al. 2012) and 1.4 to 1.5 in *Pseudodiaptomus annandalei* (Dur et al. 2010).

3.2 Multifractals as a Diagnostic Tool to Assess a Family of Swimming Behaviours

The strongly non-Gaussian fluctuations perceptible in zooplankton successive displacements that range from very likely slow steps to rare and extremely rapid displacements (Fig. 1b) are inherently incompatible with classical self-affine approaches based, e.g., on the scaling behaviour of the power spectral density described above that are fundamentally limited to second-order moments. A more general approach is based on the analysis of qth order long-range correlations in displacements. Specifically, the norm $\|\Delta X_\tau\|$ of the three-dimensional displacements of a zooplanktonic organism is defined as

$$\Delta X_\tau = \sqrt{\left(x_{t+\tau} - x_t\right)^2 + \left(y_{t+\tau} - y_t\right)^2 + \left(z_{t+\tau} - z_t\right)^2} \ ,$$

where τ is the temporal increment and (x_t, y_t, z_t) and $\left(x_{t+\tau}, y_{t+\tau}, z_{t+\tau}\right)$ are respectively the positions of the organism at time t and $t+\tau$. $\|\Delta X_\tau\|$ is a nonstationary process with stationary increments; its statistics do not depend on time, t, but on the temporal increment τ (Rutherford et al. 2004; Seuront and Stanley 2014). The moments of order q ($q > 0$) of the norm of three-dimensional displacements $\|\Delta X_\tau\|$ depend on the temporal increment τ as

$$\Delta X_\tau^{\ q} \propto \tau^{\zeta(q)} \qquad (4)$$

The exponents $\zeta(q)$ are estimated as the slope of the linear trend of $<\Delta X_\tau^{\ q}>$ vs. τ in log-log plots. The function $\zeta(q)$ characterises the statistics of the random walk $\|\Delta X\tau\|$ of the organism regardless of the scale and intensity (Rutherford et al. 2004; Seuront and Stanley 2014). Low and high orders of moment, q, characterise, respectively, smaller and more frequent displacements and larger and less frequent displacements.[4]

The shape of the function $\zeta(q)$ can be used as a direct, objective and quantitative diagnostic

tool to unambiguously identify the type of motion exhibited by zooplankton organisms and ultimately any swimming organisms (Fig. 3c). Briefly, for Brownian motion, $\zeta(q) = q/2$, and fractional Brownian motion is defined as $\zeta(q) = qH$, where $H = \zeta(1)$ and the limits $\zeta(q) = 0$ and $\zeta(q) = q$ corresponding, respectively, to confinement and localisation, and ballistic motion. Anomalous diffusion occurs when $H \neq 1/2$. Specifically, super-diffusion occurs when $H > 1/2$ and sub-diffusion when $H < 1/2$. For finite-length Lévy flights, the function $\zeta(q)$ is bilinear with $\zeta(q) = q/(\mu-1)$ for $q < \mu-1$ and $\zeta(q) = 1$ for $q \geq \mu-1$; the exponent μ ($1 < \mu \leq 3$) characterises the power-law tail of the probability distribution of the move-step length l as $P(l) \approx l^{-\mu}$, where $1 < \mu \leq 3$. For $\mu \geq 3$, the mean and the variance of the move-step lengths are both finite; hence, as a consequence of the central-limit theorem, their distribution is Gaussian. For $1 < \mu < 3$, the scaling is super-diffusive; the value $\mu = 2$ corresponds to a Lévy flight (i.e. the swimming behaviour is tailored to minimise the distance travelled whilst locating prey). Finally, a function $\zeta(q)$ that is nonlinear and convex is indicative of a multifractal random walk (Rutherford et al. 2004; Seuront and Stanley 2014).

The only study that used multifractals to assess the behavioural response of zooplankton to water contamination led towards an increase in *Pseudodiaptomus annandalei* behavioural complexity under conditions of stress induced by the presence of a diatom toxin (Michalec et al. 2013a, b). Specifically, *P. annandalei* swimming behaviour is very close to a (monofractal) ballistic motion in control water and progressively diverges towards an increasingly multifractal behaviour with increasing toxin concentrations.

4 Conclusions

The behavioural approach discussed in this contribution to assess zooplankton stress from the geometric and stochastic properties of their motion behaviour has the potential to become an efficient tool in zooplankton ecotoxicology as a sensitive, non-invasive and robust behavioural sublethal endpoint with short-response times

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[4]Note the one-to-one correspondence between the function $\zeta(q)$ and the spectral exponent β for $q = 2$, i.e. $\beta = 1 + \zeta(2)$ (Seuront 2010a).

for toxicity bioassays, in particular as it is very sensitive to subtle behavioural changes that may be undetectable to other behavioural variables (Rutherford et al. 2004; Coughlin et al. 1992).

Zooplankton behavioural complexity typically decreases under stress (Seuront 2010a, b, 2012; Seuront and Leterme 2007; Michalec et al. 2013a, b). Increases in complexity have, however, also been observed under certain stress conditions (Shimizu et al. 2002; Michalec et al. 2013a, b),[5] although such results seem to occur in response to acute or stimulatory challenges, quite apart from the chronic or inhibitory stressors that are associated to reduction in complexity (Alados et al. 1996; Seuront 2010a, b, 2012). As shown for several fractal and multifractal measures of environmental complexity (Seuront 2010a), regardless of the direction, it is ultimately the relative differences between the fractal and multifractal exponents observed for a given species under stressful and non-stressful conditions that may be more informative on the related behavioural changes.

Note that the approach described in this contribution is not limited to behavioural ecotoxicology but can be generalised to assess relative changes in the behavioural complexity of marine invertebrates in a wide range of ecologically relevant situation related to, e.g., the quality and the quantity or food and the presence of mates or predators (Seuront 2010a, b; Schmitt et al. 2006). It is finally stressed that the application of fractals to zooplankton behavioural ecology in general (Rutherford et al. 2004; Seuront 2011) and to zooplankton ecotoxicology in particular (Seuront 2010a, b, 2012; Shimizu et al. 2002; Michalec et al. 2013a, b; Seuront and Leterme 2007) is, however, still in its infancy. Further work is needed to entangle the fractal complexity of behavioural properties and to generalise the use of fractal and multifractal approaches to stress assessment in marine invertebrates.

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[5] It is worth noting that the increase in the complexity of *Daphnia magna* trajectories in contaminated waters must be treated with caution as some of the fractal dimensions reported fall outside the theoretical range $1 \leq D \leq 2$, i.e. $D > 2$ (Shimizu et al. 2002).

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