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Minireview

On uses, misuses and potential abuses of fractal analysis in zooplankton behavioral studies: A review, a critique and a few recommendations

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HIGHLIGHTS

- This work reviews uses of fractals and multifractals to zooplankton behavior.
- The basic principles behind fractal geometry are briefly rehearsed.
- Potential issues and limitations related to fractal analysis are addressed.
- Multifractals provide an objective and quantitative assessment of motion behavior.

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ABSTRACT

Fractal analysis is increasingly used to describe, and provide further understanding to, zooplankton swimming behavior. This may be related to the fact that fractal analysis and the related fractal dimension D have the desirable properties to be independent of measurement scale and to be very sensitive to even subtle behavioral changes that may be undetectable to other behavioral variables. As early claimed by Coughlin et al. (1992), this creates "*the need for fractal analysis*" in behavioral studies, which has hence the potential to become a valuable tool in zooplankton behavioral ecology. However, this paper stresses that fractal analysis, as well as the more elaborated multifractal analysis, is also a risky business that may lead to irrelevant results, without paying extreme attention to a series of both conceptual and practical steps that are all likely to bias the results of any analysis. These biases are reviewed and exemplified on the basis of the published literature, and remedial procedures are provided not only for geometric and stochastic fractal analyses, but also for the more complicated multifractal analysis. The concept of multifractals is finally introduced as a direct, objective and quantitative tool to identify models of motion behavior, such as Brownian motion, fractional Brownian motion, ballistic motion, Lévy flight/walk and multifractal random walk. I finally briefly review the state of this emerging field in zooplankton behavioral research.

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1. Introduction

According to the titles of several seminal monographs, such as '*The fractal geometry of Nature*' [1] and '*Fractals everywhere*' [2], fractal properties may be expected everywhere. Fractals have indeed early been suggested as a design principle in biology, as a fractal design is structurally and functionally efficient as it requires little energy to sustain itself [3]. It is hence not surprising that fractal structures have been found everywhere in nature. The Web of Science (accessed March 4, 2015) returned 23,249 and 54,024 articles respectively containing the word *fractal* in their title and topic between 1967[1] and 2015. Fractals are hence a prolific topic, and have found applications in nearly all scientific fields, including terrestrial and aquatic ecology – see Ref. [6] for a recent review – behavioral studies in general and zooplankton behavioral ecology in particular (Fig. 1).

The word plankton has first been coined by the German physiologist Viktor Hensen (1835–1924) [7] from the Greek adjective $\pi\lambda\alpha\gamma\kappa\tau\acute{o}\varsigma$ – *planktos*, wandering – to define the diverse group of organisms that live in nearly all water bodies of the planet. These organisms are essential to ocean life, as they provide a crucial source of food to many large aquatic organisms, such as fish and whales [8,9]. Plankton organisms include microbes such as viruses and bacteria (virioplankton and bacterioplankton), unicellular plants (phytoplankton) and a range of multicelled organisms (zooplankton), which mainly consists of small crustaceans as well as the eggs and larval stages of larger animals such as fish [8,9]. Most planktonic species are microscopic, but plankton also includes organisms covering a wide range of sizes, including large organisms such as jellyfish [8,9]. Though plankton organisms are typically thought to be passively drifting with currents, the quantitative assessment of the swimming behavior of even the most minute of them is increasingly thought as a critical determinant to both their ecology and their role in global biogeochemical fluxes [10–12]. Plankton behavior in general, and zooplankton behavior that is investigated in the present review, is hence a small-scale process of global significance [13]. The Web of Science (accessed March 4, 2015), however, returned a unique paper that includes the words *fractal* and *plankton* in its title, and only 42 papers include the words *fractal* and *plankton* in their topic. Similarly, only 13 papers include the words *fractal*, *plankton* and *behavior* in their topic. While this indicates that plankton behavioral research is still relatively poorly fractally-colored, it also stresses that fractally-inspired behavioral approaches have a significant potential to grow in the near future.

Fractals have been successfully applied to a wide range of marine biology and ecology topics including species diversity [14,15], the topographic complexity of coral reefs and rocky shores [16–22], the morphology of aquatic fauna and flora [23–33], the geometric complexity and allometric properties of marine snow [34–44], the temporal pattern of dissolved inorganic nutrients, phytoplankton and zooplankton [45–50], and the spatial distribution of both intertidal [51–59] and pelagic communities [60–68]. More specifically, fractals have been extensively used to characterize the searching behavior of organisms ranging from protozoa to large vertebrates such as seabirds, fish and mammals [6]. Note that while nearly 60% of the marine sciences studies based on fractal approaches have been published over the last decade (Fig. 1(a)),

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[1] When Mandelbrot, the father of fractals, defined in his seminal work, entitled "*How long is the coast of Britain? Statistical self-similarity and fractional dimensions*" [4], what will formally be coined *fractal geometry* a decade later [1,5].