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The need of hypothesis-driven designs and conceptual models in impact assessment studies: An example from the free-living marine nematodes

Gustavo Fonseca*, Fabiane Gallucci

Departamento de Ciências Marinhas, Universidade Federal de São Paulo, Av. Alm. Saldanha da Gama 89, 11030-400 Santos, Brazil

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ABSTRACT

The literature on the use of marine nematodes as bioindicators of anthropogenic impact is extensive. Nevertheless, review studies have reported a high degree of variability among results and no consistent overall pattern has so far emerged. This lack of congruence might be partially because hypotheses formulation in environmental assessment studies has been largely inductive or abductive and not deductive or hypothesis-driven. In the present study, we emphasize the need of using hypothesis-driven designs and conceptual models in impact assessment studies. Hypotheses for individual and population level studies can be derived from the dynamic energy budget model (DEB). By means of differential equations, DEB model can infer whether a stressor promotes a shift in energy allocation along the life history of the individuals. For community/assemblage level studies, the predictions of the dynamic equilibrium model (DEM) for species richness is presented and extended for abundance, evenness, taxonomic distinctness, and changes in assemblage structure and sample dispersion. While it is predicted that species richness peaks at intermediate levels of disturbances and enrichment, evenness decreases with increasing disturbances and reducing enrichment/pollutant concentrations. Based on DEM,enrichment and pollutants may promote change in community structure by favoring the tolerant species, while physical disturbances may promote sample dispersion as a result of unselective mortality. Finally, we discuss the benefits of using niche-based models to select the indicator species, instead of using classical ordination methods, twinspan and similarity percentage analysis. The selection of indicator species have to be independent from the other species and must consider the set of environmental conditions. The use of conceptual models to select the best ecological indicators is highly recommended. It allows a logical way of testing for causalities and of scaling the different studies for comparisons.

1. Introduction

Our need to comprehend the impact of anthropogenic and climate change on marine ecosystems is increasing. The oceans are under a multitude of anthropogenic stressors (pollutants and disturbances), which impacts on organisms (including ourselves) and ecosystem services are largely negative and still poorly understood (Liquete et al., 2013; Borja, 2014). Such necessity has motivated researchers to perform impact assessment studies using different target taxa and methodological approaches (Sarkar et al., 2006). In the past two decades several assessment studies of environmental change have shown the efficiency of using free-living marine nematodes as indicators of natural and anthropogenic environmental changes at the local scale (e.g. Boufahja et al., 2016; Semprucci et al., 2014; Alves et al., 2013, 2015; Losi et al., 2013; Balsamo et al., 2012; Moreno et al., 2011; Leonard et al., 2006; Kennedy and Jacobi, 1999). It is now widely accepted that marine nematodes are good indicators of environmental impacts for a variety of habitats (from estuaries and shallow habitats to the deep sea), types of disturbances (i.e. organic, physical and chemical) and temporal scales (short to long-term disturbances). It has also been demonstrated that the responses of nematodes are complementary to other benthic components (Patrício, 2012; Xu et al., 2014). It is the combination of many attributes that gives them the status of a good bioindicator: (i) they are widespread at high abundances over nearly all marine habitats and are commonly represented by many species; (ii) most nematode species have a short life cycle when compared to other benthic taxa; (iii) they show an holoben-

* Corresponding author.
E-mail address: gfonseca@unifesp.br (G. Fonseca).

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thic development; and (iv) some species/genera are tolerant to extreme conditions where most of the other taxa cannot tolerate (Kennedy and Jacoby, 1999). In addition, nematodes are easily sampled and preserved (Fonseca and Fehrlauer-Ale, 2012) and taxonomical identification at genus level based on the pictorial keys (Warwick et al., 1998) already gives detailed information to detect ecological impacts (Balsamo et al., 2012). These attributes have also allowed the performance of manipulative studies, at population and assemblage level, in which the effects of pollutants on the nematodes are isolated from potential environmental co-variables (Lira et al., 2013; Schratzberger et al., 2009; Gallucci et al., 2015).

The literature on the use of marine nematodes as bioindicators of anthropogenic impacts is now extensive. Nevertheless, review studies have reported a high degree of variability among studies (Semprucci and Balsamo, 2012; Balsamo et al., 2012; Moens et al., 2013) and no consistent overall pattern has been found. The lack of congruence has been mainly attributed to the fact that each study area has its particularities, regarding the type of disturbance, environmental conditions, and set of species. One might hypothesize, therefore, that free-living marine nematodes are good bioindicators of local conditions and they might not be appropriate to make error free predictions to new localities and situations. Another interpretation is that statistical differences observed in each study might have no ecological meaning.

One difficulty in comparing published studies where marine nematodes have been used to detect ecological impacts is that in most of them the hypotheses had been inductive or abductive, i.e. hypotheses were made a posteriori of the data collection. In this type of study, commonly termed descriptive studies, cause-effect relationship is not a priority (Casadevall and Fang, 2008). Descriptive studies have their value on situations where variables cannot be manipulated. Initial observation and induction give rise to novel hypotheses, which subsequently can be experimentally tested to provide a progressively detailed mechanistic understanding (Casadevall and Fang, 2008). In hypothesis-driven studies, on the other hand, the experimental design focuses on testing the causality and the mechanisms that generate the pattern by testing the prediction of a theoretical model. The main objective of this approach is to bring together different systems into the same frame of reference, which is accomplished by rescaling different realizations of the same phenomenon (Marquet et al., 2014).

Although there are several models in ecology, only few of them have been extensively used in environmental assessment studies. Two commonly used models are the dynamic energy budget model (DEB; Kooijman, 2000), which is normally used at (but not restricted to) lower levels of biological organization such as organisms and population; and the dynamic equilibrium model (DEM; Huston, 1979) specially used for predictions at assemblage or community level. The present study briefly introduces these two models and suggests them as baselines for hypothesis testing in environmental assessment studies with marine nematodes. Particularly for DEB, we discuss the main routes by which a disturbance may affect the energetic equilibrium of individuals. For DEM, we expand its generalities from predictions on species richness by including other commonly used community parameters, such as abundance, evenness and taxonomic distinctness. Although our evaluation focuses on marine nematodes, the current analysis is certainly valid for other groups of organisms.

2. Organization level and conceptual models

2.1. Organism and population levels

Particularly for free-living marine nematodes, organism (i.e. biochemical, physiological) and population (growth and mortality rates, maturation time, age structure and sex ratios) level studies are restricted to cultivable conditions (Fig. 1). This is so given the high numbers and small size of individuals in the field, together with the high dynamism of soft bottoms, that make it unfeasible to monitor single individuals or disentangle immigration and emigration from growth and mortality rates, respectively. Cultures of marine species are based on agar dishes and therefore limited to species that feed on agar or on the bacteria that grow on the agar (Moens and Vincx, 1998).

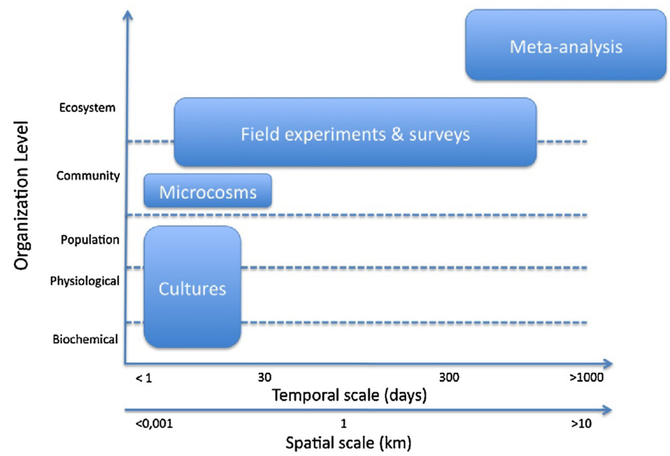

Fig. 1. Scheme relating each methodological approach with target levels of biological organization and respective temporal and spatial scales. Cultures: nematodes living on artificial cultures; microcosms: sediment samples with natural communities kept in laboratory conditions; field experiments: manipulations of variables on the field; field survey: field studies without manipulation; meta-analysis: analysis of independent data-sets.

Given these limitations, the effects of disturbance at these lower levels of organization have been poorly investigated for marine nematodes. Nevertheless, there are marine species being cultivated in the laboratory and individual level studies being conducted (e.g. Aktison, 1977; Warwick and Price, 1979; Moens et al., 1996; Moodley et al., 2008). As for terrestrial nematodes, marine species exposed to contaminants may show stress-related gene expression (Ibiam and Grant, 2005; Roh et al., 2006, 2009; Cui et al., 2007), changes in development (Rice et al., 2014), metabolism (Menzel et al., 2001; Vijver et al., 2004), behaviour (Dhawan et al., 1999, 2000; Boyd et al., 2003), feeding (Jones and Candido, 1999; Boyd et al., 2003) and morphology (Popham and Webster, 1979). Specifically for marine nematode populations, copper, lead, mercury, barium and cadmium are known to affect growth, carrying capacity and developmental time (Vranken and Heip, 1986; Lira et al., 2013). Their effects on the population parameters are dependent whether the toxic elements are in isolation or not, and when combined, the effects might be additive, antagonistic or synergetic (Vrankenet al., 1989). Additional complexity is that, as for other organisms, environmental variables such as temperature and food can alter the toxicity of trace elements on marine nematodes (Vranken et al., 1989).

Although little progress has been made for marine nematodes at these lower levels, assessment studies at individual and population levels are numerous for other organisms (Kooijman et al., 2009). The theoretical background at these levels of biological organization relies specially on the dynamic energy budget model (DEB; Kooijman, 2000). Briefly, the DEB model is concerned with how food is converted into reserve, and reserve into structure and reproduction; reserve does not require maintenance, but structure and reproduction do, mainly to fuel its turnover (Fig. 2; Kooijman et al., 2009). Therefore, DEB model assumes that a fixed fraction of the incoming energy is spent on respiration, for maintenance and