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Review

Perspective — from describing to understanding environment–physiology relations: 50th birthday of a branch in ecophysiology ☆

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ABSTRACT

Animals generally show various adaptation features that render them fit for survival in their specific environment or, turned the other way round, specific environments can only be inhabited by animals that have developed corresponding adaptations. While this seems obvious nowadays to every biologist, 50 years ago this concept still needed to be validated for each specific case. In a brief historical perspective we highlight an outstanding example of an article where such environment–physiology relations have been examined in detail and where in fact the foundations of a new branch in ecophysiology have been established, the Ecophysiology of the Marine Meiofauna.

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As is clearly documented by the establishment of *Comparative Biochemistry and Physiology* in 1960, the use of a comparative approach to physiology had already received its due appreciation 50 years ago. In addition to using diverse animals as suitable models to comparatively study physiological questions of general – and often primarily medical – interest, it seemed that more and more researchers became interested in understanding their objects of study in their own right, i.e., it became increasingly interesting and fascinating to unravel why animals would show a specific physiological feature and how this relates to the conditions they experience naturally. Thus, the next step from strictly comparative to ecological physiology, or ecophysiology, was already underway, but still in its infancy. In order to document one example of the early approach to ecophysiology that would break the ground for the entire branch, we want to highlight one article that appeared at the time CBP was founded, and even though it was published in a different journal, it was definitely co-authored by scientists that represent outstanding examples of comparative physiologists and ecophysiologists, Wolfgang Wieser and John Kanwisher.

Typically animals show diverse adaptation features that render them fit for survival in their specific environment or, turned the other way round, specific environments can only be inhabited by animals that have developed corresponding adaptations. As obvious as this may seem nowadays to every biologist, it was only 50 years ago that this concept still needed to be validated for each specific case. For this reason Wolfgang Wieser and John Kanwisher could open the introduction of what today would be considered a typical ecophysiological account with the statement: "The physiology and the physiological–ecological relationships of the small invertebrate (meiofauna) communities of marine substrates have never been investigated" (Wieser and Kanwisher, 1961).

Given that (as of June 2010) this work has been cited 101 times since its appearance in 1961, with the latest citing paper dating from 2009 (Levin et al., 2009), it appears that this study has indeed filled an important gap of knowledge and represented an important impulse with continuing impact on the field that has since then developed and flourished, i.e. the Ecophysiology of the Marine Meiofauna.

☆ This perspective is a contribution to the Comparative Biochemistry and Physiology Fiftieth Anniversary Celebration.

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As is apparently so often the case in science, the start of this study is the result of a combination of somewhat accidental circumstances, namely the getting together of broad-minded people with different scientific backgrounds but obviously shared interests (a taxonomist and a physiologist), the availability of know-how and techniques for the investigation of a specific parameter of interest (of oxygen consumption at low oxygen levels by use of the Cartesian Diver), and the accessibility of suitable laboratory space or, as is more appropriate in this case, of a perfect natural laboratory in the close vicinity (a small salt marsh near the Woods Hole Biological Station).

The situation prevailing at the onset of this study may best be appreciated in the own words of one of the authors, Wolfgang Wieser[1]: "This paper was the result of an unexpected and productive cooperation in the wonderful marine environment surrounding the equally wonderful Woods Hole Biological Station. I was at that time one of the few experts in the zoological community on free-living marine nematodes, having written a four volume monography of this group which due to its abundance and diversification offers endless challenges to taxonomists, ecologists and physiologists. John Kanwisher was a physiologist (student of Pete Scholander), with an unlimited skill for tinkering and building fabulous instruments. He owned a number of patents on diving apparatus. I had a two years grant for doing research in Woods Hole and John had a position at the same Institution. We knew from the beginning that if we are lucky our cooperation might open an almost untouched and fascinating field of marine research, i.e. the "Ecophysiology of the Marine Meiofauna" ("meiofauna" referring to the groups of animals in the size range between bacteria and small invertebrates). I had already been fascinated by the incredible diversification of this group of animals in which the basic morphology of all species is nearly identical — with exception of the feeding apparatus. I had just published a paper on the relationship between the structure of this apparatus and the ecology of a large number of species (having described and drawn by that time about one hundred new species). This may sound an awful lot, but one has to realize that the nematode fauna of marine bottoms was at that time almost unknown and that later estimates suggested that there may be something like 100,000 species in these marine habitats — a number that turned out to be an underestimate. I had hoped that with John's abilities it should be possible to measure oxygen consumption of the nematodes living in different types of bottom, ranging from sand to mud. On the basis of my work on the feeding apparatus I had already distinguished between four or five types of feeding strategies, ranging from suction feeders to predators. I wondered whether the differences in morphology and behaviour might also be reflected in differences of the rate of oxygen consumption. An additional, but as it turned out, most important factor proved to be the oxygen content of the original habitat, ranging from fully saturated in sandy bottoms at low depth, to no oxygen (anoxia) in deep mud."

So the preconditions were ideal from the strictly scientific point of view, i.e. experienced researchers were set to tackle a still largely unexplored question leading to potentially highly exciting insights. However, as mentioned above, an additional indispensable ingredient for a successful project is the availability of suitable technology, the lack of which is often the main factor hampering the progress of science. In this specific case, however, this was obviously not the case: "As luck would have it, already before my arrival at Woods Hole John had been playing with various types of respirometers, among them the "Cartesian Diver", designed for measurements at low to very low oxygen contents in the medium. As our project proceeded we became very efficient in collecting bottom samples, extracting and cleaning living worms, cleaning and calibrating small glass vessels in which the worms were maintained, and connecting the vessels to the extremely sensitive manometer of the Diver which would register extremely small changes of air pressure in the system from which the rate of oxygen consumption by the worms could be calculated."

With all necessary things set, the authors were thus able to pursue the obviously ongoing efforts of Wolfgang Wieser to correlate physiological parameters of the organisms he had previously morphologically classified with the corresponding niches they inhabited. To start out, the authors characterized the habitat with respect to the physical structure and oxygen levels prevailing in the various layers of the sediment, as well as the species composition and the population density of the nematode fauna present at the study site, both in spring and fall, adding yet another ecological dimension to their project. They discovered that while the sediment was largely anoxic below 1 cm depth, a large abundance of nematode species was detectable both above and below this threshold. In line, these nematodes also showed considerable stamina when exposed to prolonged anoxia in the lab. In addition, however, the authors found that "despite the fact that all mud-inhabiting nematodes must be able to live anaerobically for some time, they can be kept for long periods in a well-aerated medium". A closer inspection of the environmental conditions prevailing at the study site allowed authors to predict that "Since the water overlying the Penzance Point mud at high tide is saturated with oxygen and stirs to a varying extent the top layer of the substrate, there must exist at times a mud–water interface in which the oxygen content falls from saturation to near zero and in which, consequently, nematodes have the opportunity of using oxygen for their metabolism" (Wieser and Kanwisher, 1961). The authors thus determined oxygen consumption rates in 17 species of these mud-inhabiting nematodes and in addition analyzed the different physiological and environmental parameters that might affect these measurements. Nowadays, even though exact measurements of oxygen consumption rates at very low oxygen tensions are still a considerable and artifact-prone challenge (Scandurra and Gnaiger, 2010), several O_2-electrode based oximeters are capable of measuring respiration rates in hypoxic media not only in a closed chamber (as the Cartesian Diver), but also in open systems where respiration rates can be measured at relatively constant partial pressures of oxygen (Ortmann and Grieshaber, 2003). In the late 50s, however, the use of the Cartesian Diver required oxygen consumption rates to be estimated in aerated water. Thus to interpret respiration rates of these animals authors had to assume that the energy requirements for nematodes were similar in aerobic as well as anaerobic conditions, arguing that "the only indication that this is so comes from our repeated observations that the nematodes in question show identical speed and type of movement in an aerated dish and in a Thunberg tube with a highly reduced substrate" (Wieser and Kanwisher, 1961). In addition, reflecting a scientifically healthy critical view on the methodological constraints, the authors pointed out that "it is likely that in an undisturbed natural substrate, the animal would spend less energy than it would in a drop of water at the bottom of a Cartesian diver". The idea that nematodes from anaerobic muds are equally active in aerobic and anaerobic conditions was later used by Teal (1962) to evaluate the energy flow of various mud dwelling forms of another natural ecosystem. By contrasting oxygen consumption rates with the density of animals and biomass the authors were then able to estimate the total respiration of the nematode fauna – a measure of energy utilization – per unit of surface area. As pointed out by Teal (1962), this study therefore was also one of the first to allow for assessment of total energy flow of an ecosystem.

At the level of individual species the question arose as to what extent aerobic metabolism can be adaptive in these organisms. When analyzing the apparent heterogeneity in oxygen consumption rate of the different nematode species under study, Wieser and Kanwisher had to first discount several factors that might explain the apparent variability in the observed results. By comparing respiration rates for animals collected in different seasons, they showed no changes due to

[1] This and subsequent long quotes are excerpts from a letter sent by Wolfgang Wieser to G.K. in October 2009 upon request to share his recollections on the article discussed in the present perspectives article.

thermal compensation (animals simply conform to a given environmental temperature), so that the above mentioned variability in oxygen consumption rates could not be explained in terms of species-specific patterns of thermal acclimatization. The authors also noticed that differences in metabolic rates were not due to differences in size, since "species differ only little in weight and not at all in surface/volume ratio". After considering several other aspects, the authors turned their attention to the previously developed classification of nematodes into feeding groups according to the buccal cavity structure (i.e., small and large; armed with teeth vs. unarmed), referred to as Wieser's trophic theory (Wieser, 1953), widely used since then and adjusted in subsequent years (Wieser, 1960; Wieser and Kanwisher, 1961; Boucher, 1973; Platt, 1977; see Jensen, 1987). Wieser and Kanwisher used these different buccal cavity morphologies to establish a correlate with aerobic metabolism: "If the shape of the buccal cavity is pictured alongside a list of species arranged according to levels of oxygen consumption, it is found that large buccal cavities are typical of species with high oxygen consumption, small buccal cavities of species with low oxygen consumption" (Wieser and Kanwisher, 1961). Thus, a given buccal cavity would define a given feeding strategy, and this in turn would correlate with specific amounts of energy spent in metabolic and behavioral functions, so that, e.g., "species with large buccal cavities may be non-selective deposit feeders and ingest a large amount of material of which they use only a fraction", thus displaying a relatively high respiration rate (Fig. 1). Other factors such as selective digestion and morphological and histochemical differences in the intestinal cells related to the efficiency of food absorption in a variety of nematodes (Jensen, 1987) provided further support for a causative link among buccal cavity morphology, feeding habits and aerobic use of metabolic energy.

In a further insight into the ability of species to detect and move along environmental gradients, Wieser later showed that for many invertebrate species of the meiofauna, the distribution in the field quite often corresponds to the tolerance range so that e.g. the time a given species can endure anoxia is similar to the time in which it is exposed to natural microxic–anoxic conditions in a tidal cycle (Wieser, 1975, see Fenchel, 1978).

Fifty years after this seminal work was published, the above described findings could be seen in a broader context as the first attempts to link the field work of many marine ecologists and limnologists with that of physiologists interested in the metabolic plasticity of animals adaptating to aerobic–anaerobic transitions. In the words of Wolfgang Wieser: "An additional bonus of our study was that by experimenting with nematodes living in nearly anoxic (oxygen-free) sediments we were accepted by the group of zoophysiologists who were interested in anaerobic metabolism and the events taking place when animals switch from aerobic to anaerobic metabolism — and vice versa. Considering the effects of declining water quality in rivers, lakes and marine environments, this is an extremely important topic. On the other hand, it was obvious that we achieved not more but to scratch a thin layer of wisdom from a huge body that probably will remain undisturbed for some time. We discussed our results at the Woods Hole seminars and I gave a lecture at the University of North Carolina where my suggestion to organize an international project for extending our approach on a comparative level, was received with enthusiasm, but as expected died as quickly as it was borne…"

As may be seen from the already mentioned more than 100 articles that cited this work in subsequent years it is obvious that at least the general idea did not at all die off, but that the concept of examining the relation between environmental peculiarities and the physiological features of their inhabitants in fact became an important aspect of biological studies aiming at understanding the biology of ecosystems. In modern textbooks of Comparative Physiology, Ecology and – of course – Ecophysiology this concept thus forms an indispensable part

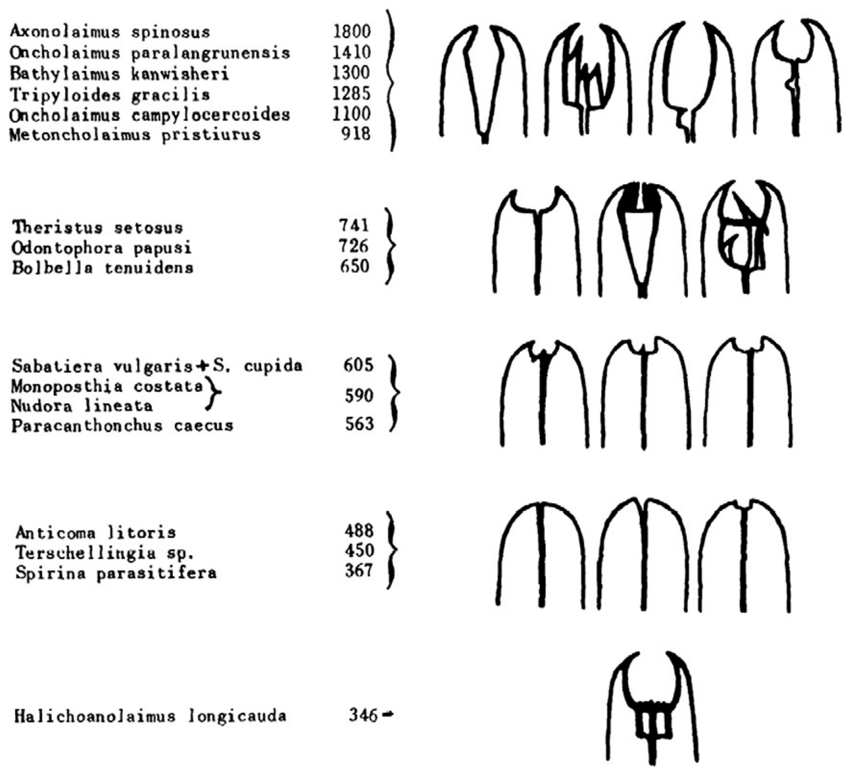

Fig. 1. Average respiration rate, in mm^3 O_2/g/h, of nematode species from Penzance Point marsh near Woods Hole, Mass., together with outline drawings of anterior end of species studied in order to show relationship between respiration rate and shape of buccal cavity. Reprinted with permission from Wieser, W., Kanwisher, J. 1961. Ecological and physiological studies on marine nematodes from a small salt marsh near Woods Hole, Massechusetts. Limnol. Oceanogr. 6:262–270. Copyright 1961 by the American Society of Limnology and Oceanography, Inc.

that is not only important from a scientific point of view, but is, at least in our personal experience, one of the most exciting aspects of physiology.

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