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PLANKTOLOGY, HISTORY, AND ECOLOGY: TOWARD AN INTEGRATED VIEW

Bernardo Barroso do Abiahy
Pós-Graduação em Ciências Biológicas (Zoologia), Instituto de Biociências, Universidade de São Paulo, Rua do Matão, Travessa 14, 321, 05508-900 São Paulo, Brazil.

ABSTRACT

Planktologists are urged to reorient their research priorities within the realm of ecologically-oriented studies according to the incorporation of a phylogenetic/historical perspective to such studies, as well as to review which are the significant problems to be tackled. In this paper I go over the most basic thematic and methodological problems that planktologists have to face when dealing with the multidimensional nature of plankton. In order to approach this subject, there is an explicit reference to the importance of using the principles of phylogenetic systematics in the planktological research, much like what has already been proposed for other fields of the biological sciences.

Keywords: Planktology, systematics, phylogenetic perspective, ecology.
Descritores: Planctologia, sistemática, perspectiva filogenética, ecologia.

INTRODUCTION

A perennial problem in a scientific discipline is to identify particularly significant contributions in the enormous numbers of publications of recent decades (MCINTOSH, 1989). This situation can be readily perceived impregnating both general and specific knowledge produced by ecologically-oriented studies of planktonic taxa (colectivelly termed here as "planktology", that is, the study of biotic and abiotic factors that possibly determine the distribution and abundance of planktonic organisms). The elements that build such a scenery are: (1) the theoretical distributions which support statistical procedures of population parameters are widely apart from both the spatial complexity of plankton and its multidimensional nature (VENRICK, 1978), (2) the conventional sampling methods woefully inadequate for addressing many of the most crucial questions, not only in larval ecology, but even in holoplankton ecology (GREENE, 1990), and (3) the lack of ordered knowledge about plankton history and evolution according to updated systematic approaches.

Plankton comprises an array of different organisms, including microscopic and macroscopic life represented by bacteria, algae, and an immense group of animal species, from lower invertebrates to juvenile forms of aquatic invertebrates and vertebrates. A real bottleneck admittedly associated to the study of plankton is the capacity of a great part of it to show clear signs of autonomous vertical and horizontal migration at a certain extent, thus extremely depreciating the effectiveness of sampling strategies. For this reason, when I speak of "planktology" or "planktonic organisms" I will be basically referring to marine and estuarine zooplanktonic taxa, especially because they are in a much worse position to have patterns of abundance, occurrence and distribution accurately determined in face of their unknown potential to accomplish such migration movements (KERFOOT, 1980).

The way of acknowledging and understanding the diversity of plankton has still to be stuck to collecting methods that are essentially the same ones once employed since mid-nineteenth century (WICKSTEAD, 1976). Methods commonly used for monitoring plankton usually neglect the fact of patchy distribution, and thus results suffer, as pointed out by DE WOLF (1989). Also, he proceeds, interpretation of such data can be highly misleading, particularly when used to assess the environmental status of an area: an overestimate or underestimate of population density may be the result. Marine planktonic copepods, for instance, have been observed many times in great numbers, but precise count per unit volume is elusive, considering patchiness, vertical migration and zonation, and other factors (HUMES, 1994).

Crucial to planktology is how informative are data based on the pitfalls and drawbacks inherent to sampling strategies in the field, as well as on the arbitrary criteria supporting such strategies. For example, the incapacity of sampling one same population repeatedly (temporal analyses) or sampling different sites simultaneously (spatial studies) imposes an element of spatial-temporal interaction difficult to be extracted from the set of data (IBANEZ, 1973a, b; 1976).

It must not be overlooked the general trend in the biological sciences of recognizing consistent systematic studies as the fundamentals of comprehensive hypotheses in any field of research dealing with living organisms. NELSON (1987) really meant that when he stated: *"Biology is unique because it studies life that has evolved; life is the way it is because there has been an evolutionary history. This is not to say that great discoveries are not made by workers who ignore the evolutionary history of life - obviously they are! But one of the great contributions of biology is in finding out how the various carriers of, for example, behavioral and physiological traits have evolved and are related to other forms. For example, we want to know if certain traits have evolved independently or not...By having a good systematic understanding of life, we learn the degree to which diverse lineages handle similar problems"*.

The perception of ecological phenomena through history and evolution has been considered here one essential requirement for planktologists to enhance the scientific/informative content of their research practice. Evolution has been the unifying concept of biology for more than 130 years (BROOKS and MCLENNAN, 1991), and this is what should be basically reflected by the numerous investigations pertaining the biological sciences. Anyway, this is clearly a matter of individual choice, and of course planktologists, like some other scientists, may persist in their self-appointed descriptive role delegating to others the task of deriving evolutionary meanings from their proposals (CHRISTOFFERSEN, 1995).

The premises I shall consider as the base line to conduct the following discussion are thus founded on methodological and thematic grounds. "Methodological" in this case deals with the methods of collecting plankton and interpreting data. Consequently, the question to be answered should be "How planktologists can produce significant and comprehensive knowledge while working with biased methods of collecting plankton, in the very first place, and with explicit preference for proximal explanations to account for the occurrence, distribution and abundance of planktonic organisms?".

I will work on the essence of the above paragraphs in order to keep focus on the question just posed.

PLANKTOLOGY: MEANS AND GOALS

Planktonic organisms have been studied for around a century and a half according to a general descriptive approach both in taxonomy/systematics and ecology. The descriptive approach in taxonomy/sytematics emphasizes morphological aspects of the animals, while in ecology the **main** *focus* is the search for proximal causes (abiotic and biotic factors) possibly determining the occurrence, distribution and abundance of populations' individuals. Actually the work of planktologists is much like the one usually pertaining to the population ecology field, and thus TWOMBLY'S (1994) consideration quite fits the present context: "*One of the major goals of population ecology is to identify the factors that regulate patterns of distribution and abundance of an organism. A commom approach to this problem is to correlate changes in population size with changes in environmental factors and to infer cause and effect from significant correlations*".

GREENE (1990) listed the major disadvantages of the conventional sampling programs using a variety of water bottles, submersible pumps, and plankton nets as follows: (1) all conventional sampling systems are intrusive and size selective, making the selective collection of small animals and avoidance of large animals two likely source of bias; (2) all conventional sampling systems are potentially damaging, making the selective destruction of fragile animals another source of bias; (3) sample processing is labor intensive and time consuming, making near-real time assessment of zooplankton distribution virtually impossible; (4) net sampling systems typically integrate out small-scale distributional features, making it difficult to assess the importance of such features on various ecological processes. TURNER (1994) touches upon these recurrent problems showing results of other studies on copepod distribution and his own experience: "*The reason for this discrepancy is probably differences in meshes of nets used for collection. The studies reporting larger copepods as dominants used meshes of 333-505µm, whereas those reporting small copepods as dominants used meshes < 153µm. Thus, had a mesh larger than 102µm been employed in this study, the dominant zooplankters in the system would have been severely undersampled or missed*". Additional remarks could join this summarized critical evaluation concerning the arbitrariness in the determination of number of samples, frequency and periodicity of sampling, number and place of sampling stations, and so on. Modern sample processing technology (e.g. remote sensing, sound scattering, optical sensing), which I believe work out only in peculiar investigating plans, is not being considered here since it does not belong to the day-to-day planktological research worldwide.

To date, few studies have documented biases in the estimation of zooplankton community biomass or production caused by selectivity of nets of different meshes (HOPCROFT *et al.*, 1998). The importance of small species of cyclopoids and nauplii, for example, to biomass calculations and taxonomic studies has been thus clearly neglected.

That the work of planktologists will still depend, for a long while, on the biased conventional sampling and collecting strategies is clear to me. It is also clear that, even considering this adverse situation, basic knowledge has been built for very specific contexts (e.g., description of the microcrustacean faunas of lakes, temporary waters, lagoonal systems, freshwater ponds). VAN DER SPOEL and HEYMAN (1983) were optimistic about the possibility they consider to distinguish only among an epi-, meso- and bathypelagic realm, but pointed out that we are prevented from understanding the vertical dispersal because of lack of data, chiefly due to inadequate sampling techniques. In face of this constraining reality, the most helpful insight I can wonder of to make worth value all the effort put forward in a planktological survey is bridging history and ecology through phylogenetic systematics' studies, thus rendering all sorts of speculation and hypothetical constructions about patterns of occurrence, distribution and abundance a more comprehensive and consistent status. This, for sure, demands an even tougher work and much time...

Collecting, counting and identifying planktonic organisms are typical activities in planktological research. Results of such a research are commonly integrated in an microecological context so that data collected can be correlated with environmental immediate profiles. Conclusions derived from this classical approach fail to consider the various possibilities of making more fruitful methodological and analytical procedures. LOEHLE (1987) pointed out that serious hypotheses, after all, have explanatory power: they explain phenomena in terms of history, mechanisms or evolution. General theoretical and methodological directions are already available for this in biology: the theory of evolution and the phylogenetic method. Therefore the means and goals of planktology are openly prone to profit from this perspective, expanding their boundaries beyond the descriptive and circumstantially interpretative and analytical format.

A real difficulty facing planktologists is how to determine what is relevant information that should be incorporated to a certain study assuming, of course, that a significant problem has been posed. I shall again stress that the investigator is free to choose whatever subject he or she is willing to discuss, as well as the level the debate is expected to reach. So, if one is up to describe functional processes, to report faunistic data, to quantify populational parameters within a microecological framework, this must be regarded as an important problem under target. In the case of planktology, theoretical and methodological backgrounds supporting conclusive studies of distribution and abundance are still rare (but see BAYLY, 1995, and COLBOURNE *et al.*, 1998, for a few exceptions). Therefore, there must be some additional engaging in more inclusive levels of theoretical and methodological approaches so that ecologically-oriented studies of planktonic taxa yield more comprehensive explanations.

Methods of investigating plankton ecologically (= planktology) thus can barely deal well with operational shortcomings of collecting biological material in the field. On the other hand, methods of interpreting eventual associations between hydrological and populational data can experiment a significant improvement if the planktonic organisms studied are considered to be the center of a certain ecological phenomenon. At this point, I hope a first critical message has already been clearly explicitized in favor of a higher comprehensiveness of hypotheses in planktology: the complementary nature of history and ecology. The second critical message claims for the production of consistent systematic (empirical) knowledge of organisms as the pillars for any kind of ecologically bounded scientific work. In general, I shall refer to BROOKS and MCLENNAN'S (1991) conception of linking history and ecology as the outstanding approach for planktologists to begin their explorations, which would include two pieces of information: a phylogenetic hypothesis and the relevant ecological data.

THE HISTORY X ECOLOGY DICHOTOMY

Discussion on conceptual, epistemological, and ontological problems, as well as comments about phylosophy, history, and perspectives of renewal within ecology have been intensified since the 80's (MCINTOSH, 1987; SLOBODKIN, 1992). This movement can be viewed as a fundamental step towards the scientific maturing and objective definition of study proposals within this discipline. Occurrence, distribution and abundance of organisms, considered under the scope of the biodiversity issue, turned out to be the major reference for ecologists to mold their research activities in general. Despite the difficulties in designing experiments to make more robust the empirical nucleus of ecology, suitable room is already open for methodological standardization borrowed from history-laden scientific disciplines. In the case of ecology, where relationships between organisms and physical factors are primarily on focus, a relevant amount of empirical data can be acquired if such organisms are considered in first place. To back this approach, I urge for systematic studies logically, ontologically, theoretically and methodologically consistent, uniform and updated, which I believe drives us directly to phylogenetic systematics and its implicit historical nature.

It is a well-known fact that both the geographic distribution and the speciation of plankton are products of the geological history of the oceans, the continental barriers, the current patterns, and the limitation of survival of individual species and populations by both biotic and abiotic environmental conditions (VAN DER SPOEL and HEYMAN, 1983). Planktology as a whole is a discipline which has been traditionally directed to the study of non-historical and contemporaneous processes, and a time dimension hiatus thus appear where history and ecology seem to occupy dichotomous positions. GRAY (1990) maintained that this dichotomy should be abandoned because historical influences such as geological events are mediated ecologically, and ecology is historically contingent. Instead of acting as separate independent processes on different spatiotemporal scales, he proceeded, ecology and history act together at all times. So, it is not wise to delimit the time dimension of planktology to a strict contemporaneous context which excludes the set of historical interactions ultimately defining current environmental conditions.

Again, the commitment in play should be the one of bringing ecological studies of planktonic organisms into a more informative and unifying context involving the basic questions of current distribution and abundance. "...*Ecology and population biology have been dominated by explanations rooted in processes observable today*..." (WANNTORP *et al.*, 1990), and this is viewed here as producing partial perceptions of ecological phenomena. The search for proximal temporal causes responsible for the occurrence, distribution and abundance of planktonic organisms is invariably destined to cover circumstantial spatial pictures defined in the arbitrary sampling universe established for work, specially when small systems are expected to unequivocally represent larger ones in diverse conditions (MCINTOSH, 1987).

The initiative to blend both ecology and history, thus bringing close together proximal and distant causal explanations for the distribution of planktonic organisms, is about to turn to a necessary component of comprehensive planktological studies. When hypothesizing about the geographic range of a certain species, proximal causes prove to be of very restrict use, since just the ecological time dimension is normally taken into account. The extreme difficulty in accepting distribution and abundance patterns based on biased sampling strategies should have pushed more strongly planktologists to the formulation of comprehensive hypotheses encompassing both (micro)ecology and history. Much of the work of a planktologist is dependent on questionable sampling strategies, and specially for this reason, a detailed systematic account is always wellcome to disperse shortsighted and speculative discussions on whatever aspect about a certain planktonic taxon.

The view of plankton as a product of ecological explanations is an effective demonstration of the importance given to case studies in biology. Case studies are necessary to help building progressively robust hypotheses. But to achieve this, one has to use all the potential connections between specificity and generality, punctuality and globality, non-comparativeness and comparativeness. Functional and structural ecological studies, for example, can yield significant results as far as they can bounce from each first elements to each second elements of the 3 mentioned pairs respectively. In a rather more difficult position stay the distributional studies, simply because they depend on theoretical constructions and empirical evidence of key disciplines, such as oceanography (*e.g.*, origin and evolution of the oceans and ocean circulation), structural geology of ocean basins, plate tectonics, taxonomy and phylogenetic systematics.

Among the astonishing variety of planktonic organisms, copepods stay out as very probably the most abundant and widely distributed group of metazoans in the oceans, coastal systems, and freshwater environments. An amassing amount of data has been published about their ecology, but with limited discussion on the historical processes underlying their current temporal and spatial dynamics. Information on distributional patterns of estuarine, coastal and oceanic planktonic copepods are either associated to proximal/microecological explanations or to the major current features of oceanic circulation (*e.g.*, BOLTOVSKOY, 1981; NISHIDA, 1985). With the advent of phylogenetic systematics and vicariance biogeography, terrestrial animals and plants, in general, started to be investigated under objective methodological procedures and clear theoretical assumptions, which integrated both (micro)ecology and history. However, little progress under this perspective could be noted concerning the huge number of aquatic invertebrates, planktonic copepods among them.

Species can be circumglobal, widespread or endemic in distribution, and this applies to both terrestrial and aquatic animals. In regard to terrestrial animals, integration of phylogenetic systematics with vicariance biogeography made possible a comprehensive treatment for hypotheses of species distribution, and this can also apply to both large (macroecological) and small (microecological) time-space realities. The problem of marine plankton occurrence, distribution and abundance requires equivalent treatment in order to be solved in its numerous facets. Within the scope of oceanography, the vicariance of ocean currents, if such an expression could be coined, would undoubtedly help having understood the general patterns of plankton distribution derived from history. Together with phylogenetic and ecological (functional, structural, etc) and biological (developmental) studies, a great deal of significant knowledge could thus be formed.

Vicariance of ocean currents and environments has a lot to do with early life on earth and the evolution of characters of species along parallel routes. Endemic species, be their endemism based on ecological assumptions or else, first of all have a history to tell, that is, how did they reach the place they live. So, how did *Pseudodiaptomus gracilis*, for example, come to be restricted to the mouth of the Amazonas river, while *P. richardi* spread from the same area all the way down the estuaries of the Brazilian coast, even reaching the mouth of the Prata river (BJÖRNBERG, 1981)? I believe that the adequate approach to this illustrated problem would require (1) a more careful study of the origins of the environments in which the organisms were encountered and also (2) a hypothesis about the phylogenetic relationships among the species of the genus *Pseudodiaptomus*. Tropical estuaries in Brazil are young environments probably 20 million years old (POR, 1984), and the occurrence and distribution of *P. gracilis* and *P. richardi* are initially subjected to this historical event. Relevant ecological data would then complement an eventual hypothesis for the occurrence and distribution of the two species in question, when persistent ancestral characters and adaptations within an ecological time can be distinguished from each other and, at the same time, compose a sound explanation for a determined pattern of occurrence and distribution.

I am strongly convinced that planktological studies supported by careful phylogenetic (historical) analyses and vicariance precepts result in a much more unifying, organized, updated and prospective knowledge about distributional features of planktonic organisms. But before reaching this situation, one must be well aware of the possibilities of exploring different relevant issues, about what I shall discuss next.

ON THEMATIC PRIORITIES FOR PLANKTOLOGICAL STUDIES

Thematic priorities are regarded here as the outstanding issues to be addressed in planktology according to theoretical and methodological updated trends within the biological sciences. I insist that different fields in the biological sciences benefit from the orientation provided by general unifying ideas and objective methodologies. What then?

Formally, since DARWIN (1859) biologists have been expressing increasing interest in evolution and in the methodological debate involving the objective determination of diversity patterns and processes. The previous century and the years to come before the publication of "The Origin...", however, were already impregnated by the anxious attitude of scientists towards the answer of the problem of the evolving animal and plant species, with special attention to the evolution of man, including the embriological theoretical outset (see GOULD, 1977, for a historical background). Time has passed and different lines of thought converged to a few thematic preferences: genetics (specially under the molecular perspective), ecology (with its microscale descriptive and quantitative trends) and systematics (with its empirical emphasis and evolutionary-historical appeal mainly after HENNIG'S 1950 book on phylogenetic systematics and the advent of vicariance biogeography). The year now is 2001 and evolution, more than ever, stays out as the central topic for discussion among geneticists, zoologists, botanists and ecologists.

Planktologists usually work in accordance with either the structural or the functional basis of ecology when dealing with fractions of populations. The correspondence between hypotheses explaining patterns of distribution, and the theoretical and methodological tenets of the biological sciences is a loosen one. This reveals the option of planktologists for preserving the descriptive nature of infant stages that sciences normally have to go through before reaching theoretical and methodological maturity. In other words planktologists, studying plankton functionally and structurally and within the scope of population ecology, are subject to scientific segregation if they do not find general theoretical and methodological principles with which they can associate their hypotheses.

Up to this point, it is expected that the following conflicting situation has been made clear. Plankton investigators have been producing an enormous amount of descriptive data on functional processes and structural patterns, frequently involving the relation of physical aspects of the environment to fragments of populations. However, results are strongly limited by both the nature and range of methods of collecting and analysing data and by laws, principles and theories with questionable empirical content. Planktologists seem to elect their themes for study with the only fate of description (what should be respected) but, because of this, they can only ascend to a technical level (and sometimes, it must be admitted, at expertise technical level) in their field of research. Themes for scientific research should, I believe, always have in perspective the most unifying theoretical principles and methods available at the time being what, in the case of biology, appears to be evolution and the phylogenetic method. These are multifarious aspects that have been fervently debated, in spite of being essentially preserved as strict central subjects in biology. So, if functional or structural features of fragments of planktonic populations are object of study, let us make the results of this study align with the evolutionary theory through the phylogenetic method.

The information that has (and will be) accumulated on functional processes and structural patterns of planktonic populations has been waiting for interpretative treatment in terms of evolution. However, there seems to exist an unnecessary huge gap between planktologists and systematics (= evolution and the phylogenetic method). This gap is precluding planktologists from advancing to higher levels of scientific maturity, where case studies are actually little pieces of comprehensive hypotheses yet to be proposed and justified.

To conclude on this, it should be reminded that themes for studying plankton will be regarded as priorities according to the theoretical and methodological backgrounds used for reference, and also to the level of discussion aimed (descriptive or interpretative/analytical in terms of processes and patterns of occurrence and distribution). Evolution and the phylogenetic method have been considered here as the major guidelines fulfilling these backgrounds. I shall advance now to more practical considerations on how to incorporate the evolutionary and phylogenetic perspectives to planktological studies.

PLANKTOLOGY: ON HOW TO EXPAND THE INFORMATION CONTENT OF ITS RESEARCH PRACTICE

The points discussed up until now refer to the basic idea of this section: how planktologists can improve and expand the information content of their research practice? I will try not consider this issue following a strict step-by-step procedure to reach this objective. Moreover, I expect it to be understood by now the orientation a planktologist has to consider in order to progress (if he/she wants) towards a mature theoretical status. It is important to remind, once again, that methods must be viewed not apart from the theoretical body underlying the scientific discipline being dealt with. Therefore, the phylogenetic method makes good sense when the hierarchical system of nature is accepted as an understandable entity, that is, if the ancestral-descendant relationships among organisms are believed to exist in progressive inclusive levels.

Every biological event has two factors regarding time dimension: the ecological <u>*AND*</u> the historical factors. A doubt may still persist regarding the understanding of what extent of time ecological and historical factors account for. SCHOENER (1988) helps to objectively express this abstraction assuming that, by definition, ecology concerns processes in ecological time, *i.e.* in the order of one to one hundred generations or years. History, on the other hand, is tied to events associated to large spatial scale, and thus refer to the geographical scale of regions, large scale geological units, global patterns, etc (ROSEN, 1988). These ideas are important to help establishing the distinction between, for example, an ecological succession and an evolutionary (historical) constraint on contemporary distribution and diversity, which can only be assessed with the understanding of geological history, past and present physical environments, phylogenetic history and evolutionary constraints of the taxa, the dynamics of speciation and extinction processes, and the ecological relationships of species with both their physical environment and other kinds of organisms (BROWN, 1988).

It is obvious, so, that it is not an easy task that planktologists have to face to make the results of their research correspond to significant knowledge. Occurrence and distribution of plankton is not just ecologically bounded, but also and basically, historically constrained, as life itself is. But, in case one really means to study occurrence and distribution of plankton with such a commitment, how to have this well arranged?

The limitation of working with very specific objectives in very specific contexts is that the results that an investigator reaches may serve to excessively restricted conclusions about patterns of plankton abundance and distribution. I suggest that this kind of research should consider more carefully the history of the organisms involved, so that hypotheses based on functional and structural aspects described for fragments of populations are not badly influenced by biased interpretations. As far as the history of organisms turns out to be a fundamental source of data, the method devised up to date to properly use it has been referred to as the phylogenetic method. It must be clear that the phylogenetic method is not a straightforward recipe to address historical events of cladogenesis or the relationships among organisms. Rather it is a way of reasoning about the assumption that life is historically connected throughout time, and this information can be extracted basically by the empiric study of extant and fossil forms. The phylogenetic way of perceiving life stimulated the arising of strict objective methodology to hypothesize about the origins of and relationships among organisms (*e.g.*, numerical cladistics, to account for more recent attempts).

There is no extraordinary model that planktologists can make use of so that huge fields of research such as (phylogenetic) systematics, (vicariance) biogeography and paleontology can be totally explored to yield results of incontestable meanings, and I believe that a central question has now to be considered: how can historical aspects generative of current biotas be identified and incorporated to explanations of patterns of occurrence, distribution and abundance of plankton?

The answer to this question requires a permanent attention to the overall organization of life in its various hierarchical levels. The hierarchical and nested nature of biological diversity can be perceived from every level imaginable, which can stretch from macroscopy to microscopy of parts of individuals, populations, reproductive communities, ecosystems, biotas, and so on (AX, 1996). Plankton expose this reality with a remarkable variety of examples, no matter the level being used to investigate the order of life. The Maxillopoda, for instance, display developmental paths which led to their neotenic appearance within the crustacean lineage (WALOSSEK and MÜLLER, 1998). Within the maxillopodans, copepods reinforce such paths, which historically proved to be of value for their widespread distribution in the plankton.

Species of the cyclopoid copepod *Oithona* are notably successful in both the estuarine and epipelagic oceanic plankton. During a current unfinished phylogenetic study of oithonids by this author based on morphology, a very distinctive group of species, apparently associated with oceanic waters, was soundly identifiable. In this case, morphology is giving important hints about the occurrence and distribution of some species within a historical context. Although the group is consistent with the distributional categorization proposed by NISHIDA (1985), the drawbacks of collecting techniques should always be brought into perspective.

Phylogenetic schemes are handy in many ways regarding interpretation of planktological data. The very success of calanoid and cyclopoid marine copepods in the plankton, like *Calanus* and *Oithona*, suggest a quite long history of events in terms of their ontogeny, genetics, physiology, biochemistry and morphology. Such history is frequently pinpointed in the ecological research of plankton, in turn developed within an adaptationist framework. To verify that oithonids are replaced by cyclopids as one goes from marine to freshwater habitats is some kind of observational exercise, but crucial for the understanding of this phenomenon is the set of hypotheses explaining consistent historical patterns that led to current ones. This is well defined in phylogenetic hypotheses (WANNTORP *et al.*, 1990).

Around 20 million years ago, tropical estuaries originated (POR, 1984). Numerous ancestral populations invaded these geomorphological and biological dynamic systems. Those that succeeded obviously selected a set of genomic features through a long period of time that guaranteed their success, which means that a series of ecological events in the history of such systems, evolving together with the genome of the organisms, determined the distributional and diversity patterns currently known. Preliminary results of the phylogenetic analysis mentioned above, based on morphology of oithonid adult females, suggest that the identity of an amazonian group of species (*Oithona bjornbergae*, *O. amazonica*, and *O. bowmani*) might have been derived from an oceanic ancestral, characterizing a secondary freshwater invasion.

The hypothesizing of the evolution of ancestral developmental, genomic, molecular and/or biochemical traits of a certain taxon is not a decisive approach to address all the significant ecological questions. However, BRAGA *et al.* (1999), using molecular data to investigate the phylogeny of Euchaetidae (Calanoida), proved that phylogenetic hypotheses are valuable to account for the distribution of members of this family, showing possible recurrent invasions of plankton in freshwater environments.

It is very clear that a set of variations observed in a taxon can help demonstrating both general and specific trends in its occurrence and distribution. Assuming that oceanic oithonids are more morphological derived then coastal and estuarine forms does not answer the question about their particular ecological requirements, but adds complementary important historical explanations that can be tested according to different sources of data (morphological and molecular, for instance), and progressive rigorous character analyses.

Planktonic life has been classicaly considered to be derived from benthic and epibenthic ancestors that lived in shallow seas. Morphology shows that this might well have been the case in general terms. Loss of elements and extreme specialization of oral appendages are examples that run along this line. All this can be inferred by analysis of varying characters assuming that species are historically connected through ancestral-descendant or hierarchical relationships.

SOME WORDS ON PHYLOGENETIC SYSTEMATICS

A good beginning to introduce this subject comes with HENNIG (1965): "...*Since the advent of the theory of evolution, one of the tasks of biology has been to investigate the phylogenetic relationship between species. This task is especially important because all of the differences which exist between species, whether in morphology, physiology, or ecology, in ways of behavior, or even in geographical distribution, have evolved, like the species themselves, in the course of phylogenesis. The present-day multiplicity of species and the structure of the differences between them, first become intelligible when it is recognized that the differences have evolved in the course of phylogenesis: in other words, when the phylogenetic relationship of the species is understood...*". Apart from one's personal preferences and beliefs on methods, purposes and practice of studying whatever type of organism past or present, Hennig's point of view is a concise appreciation of an updated worry spread among various systematists, biogeographers and paleobiologists that should be taken into account by those working with patterns and processes centered on fragmentary microecological time scales, as planktologists usually do.

The race started by systematists to figure out the one most reliable method to infer phylogenetic relationships among organisms has pushed ecologists and systematists too much apart. Therefore, the interest in basic questions about the evolution of populations to which individuals belong remain largely unexplored by planktologists. Worse than that, the possibility of working with a diversified nature of data under a phylogenetic perspective has been just ignored in the bulk of planktological research. ROSEN (1988) reminds, however, that phylogenetic methods are unique as a group because they provide direct historical hypotheses even from a single (non-synoptic) data set, and I believe this to be a precept of general methodological applicability that one can work with. It is necessary to quote BROOKS andMCLENNAN (1991) to stress the two pieces of information that the planktotologist, who is up to work according to a historical/phylogenetic perspective, must begin his/her exploration: a phylogenetic hypothesis and the relevant ecological data.

The phylogenetic methodology was devised by HENNIG (1950) and had to undergo a latent period of a couple decades to prove its value for biological systematics and, consequently, to biology as a whole. Extensive considerations were put forward upon the scope of such methods on theoretical, epistemological and ontological grounds (*e.g.*, WILEY, 1981; MINELLI, 1993; AMORIM, 1997). The importance of taxonomic plus phylogenetic studies for the interpretation of particular patterns of occurrence, abundance and distribution has been thus properly discussed. In other words: if consistent patterns of occurrence, abundance and distribution of organisms are detected, there is an evolutionary process underlying such patterns that needs to be comprehended, which in turn is expressed in the phylogenesis of the species. Again, BROOKS and MCLENNAN (1991) help us put clearer this idea stating that the ecology of any given species in a community may reflect the presence of persistent ancestral states or of recently evolved, autapomorphic traits, all that being potentially assimilated by the historical and non-historical components of phylogenetic analyses.

Hennig's major contribution [to vicariance biogeography] was the development of a method of analysing taxa with respect to shared characters which have been derived from an ancestor common only to themselves (shared derived character states or synapomorphies) (SCHOENER, 1988). Character states perceived in extant species, be they related to either functional or structural aspects of groups of individuals within populations, have to be regarded as the most recent cut in the phylogenesis of species, and shall not be analysed solely on the descriptive basis of their current expression (morphological/phenotypic, physiological, genetic, biochemical, ecological, etc.). Living things have special properties and requirements because they share histories in common environments and constraints owing to common ancestry (BROWN, 1988), and all that can be addressed by phylogenetic hypotheses. That is why they are so important to the understanding of the microecological reality oftenly focused by planktologists.

It was not my purpose here to discuss in detail the methods and principles of phylogenetic systematics. I just tried to call attention to the reasoning that supports them. For the ones who keep interested in describing plankton on its functional and structural basis, some ideas about the general utility of this reasoning specifically in the planktological research definetely need to be articulated next.

ECOLOGY AND SYSTEMATICS: TIME TO BRIDGE GAPS

Throughout this text, I have quoted a few investigators worried about the problems of occurrence, abundance and distribution of species (basically systematists, biogeographers and ecologists). All such problems have been gradually more closely attached to general biodiversity issues. Surprising as it may seem at first to a few readers, these problems have been prospectively approached with the aid of phylogenetic methods (ELDREDGE, 1992). Still, the question of how to deal with historical and regional causes influencing occurrence, abundance and distribution of species has been an almost exclusive encumbrance stimulating systematists, historical biogeographers and paleontologists, but not those working with the ecological reality in general.

One point has to be clear about the eventual utilization of phylogenetic methods by non-nomothetic empirical disciplines, like planktology has proved to be: there is no straightforward protocol adapting phylogenetic methods to planktology. Rather, planktologists have to incorporate and exercise the phylogenetic reasoning upon which past and current methods dealing with diversity were and have been developed. In other words, one should be able to have a look at a distribution checklist of marine copepods, for example, and envision a pathway to help interpret the occurrence of species A in the Antarctic and Arctic Oceans and of species B along the tropical estuaries of South Atlantic. This can only be done through analytical methods that incorporate both historical and ecological components of diversity, as the ones constructed according to the principles of phylogenetic systematics.

There is an implicit point to the constant reference in favour of historical explanations about diversity: the organisms that planktologists study are not stuck to their present space and time scales, and I believe that planktologists are well aware of this. So, returning to the example in the above paragraph, let me unfold the assumed question in the following way. After checking and rechecking populational parameters and hydrological factors, someone verified that the cyclopoid copepod *Oithona pseudofrigida* has a circumpolar distribution due to its close relationship to a certain water temperature, associated to some index of primary productivity, oxygen concentration, presence of a certain type of prey, etc.. Now, after all the results laboriously put together, what conclusions about the occurrence, abundance and distribution of this species one can be led to? Probably the ones redundantly showing that *Oithona pseudofrigida* is encountered in these kinds of environments because water temperature was..., primary productivity index was..., oxygen concentration was..., prey relative abundance was..., etc.. I surely do not dispute the utility of this kind of information, but I think this is too little to be pursued when so many causes beyond the proximate ones are involved in the patterns of occurrence of species. Of course, this is a crude example of what is a research activity of a planktologist, but what if these essentials are not open to discussion at all?

I shall remind the reader, once more, that what has been criticized here is the option for an exclusive descriptive framework that is clear in the literature about plankton occurrence, abundance and distribution, both in its ecological functional and structural basis. The mere interpretation of the results of such type of scientific production cannot be taken as the ending point of such production. It is the same as being satisfied with an immature level of scientific research.

DOBZHANSKY's (1973) assertion that "*Nothing in biology makes sense except in the light of evolution*" cannot be taken as a definite proposition that has to be rigidly followed by biologists in general. However, we shall concern ourselves with progressive levels of comprehensiveness of hypotheses and explanations in biology, and I see Dobzhansky's viewpoint as a straight push toward the accomplishment of this attitude. It has been generally assumed that a "full" (or at least "close to a full") explanation in biology should encompass an evolutionary explanation. However, evolutionary explanations can be viewed as dependent on previous functional or structural explanations in which descriptive approaches are priorized. Therefore, the following picture comes out: planktologists, who describe ecological functional and structural features of plankton populations, have consciously opted for the production of first-level explanations to their problems, leaving up to evolutionary biologists (basically systematists) the task to give their explanations a proper level of conclusiveness and comprehensiveness (second-level explanations).

I want to remind that, although I wish to see ecological explanations accompanied by ampler interpretations about patterns of diversity regarding planktonic organisms, I sincerely keep on respecting descriptive work in biological sciences as significant ones. Also, I want to stress once more that the reasoning that stays back the phylogenetic principles is the one that a biologist should strive to follow; something really beyond methodology alone. In other words, methods are just tools serving to conduct us to the resolution of specific problems. I am much more concerned with the reasoning upon which methods are dependent.

The proximity of planktologists to systematics and evolution is, I believe, an urgent requirement to yield a planktological research more tuned with the essential questions of biology. Phylogenies of a numerous amount of zooplanktonic groups are badly needed to help constructing informative knowledge about the nature of such groups. So, it is not a matter of applying or employing the phylogenetic/cladistic method to ecology as an easy and fabulous recipe leading to prospective results. A phylogenetic hypothesis has first to be drawn with regard to the organisms, or their morphology, physiology, genetics, ecology, etc. Of course, the greatest part of the information to be gathered on these fields will be subject to a permanent state of reviewing, checking and complementing procedures according to the concepts and ideas eventually presented, a necessary and healthy aspect of gradually more consistent data interpretation and hypotheses testing. Phylogenies of copepod orders, for instance, have been restricted to a few proposals in the 1990 decade (HO, 1990; HUYS and BOXSHALL, 1991; HO, 1994). If one has a closer look in more exclusive taxonomic groups, regarding planktonic organisms, the situation appears patchy as well.

Systematics, as I am led to conclude, has still been treated as a discipline which fate is just to solve nomenclatural problems that are posed to those who are not "specialists" or are not interested in the task of identifying species. I think this has turned out to be the one practical obstacle hampering a more informative way toward the development of a varied group of research practices in the biological sciences, the planktological one being among these. DE PINNA (1991) calls attention to the role of systematic research, stating that systematics is a general comparative method that permits an assessment of the generality of biological phenomena. From these generalizations there comes a whole array of implications for studies on evolution of taxa and characters, biogeography, coevolution, and other fields that can fruitfully develop upon taxonomic patterns. "*Consequently, systematics has the status of a metascience, providing a basis for many, perhaps potentially all, biological disciplines*" (DE PINNA, *op. cit.*).

The view of systematics as a metascience has not yet been accepted by most scientists dealing with the problems of diversity of life in all its facets. To be more inclusive, shifts in both the ontological and logical basis of systematics have required biologists to assume more critical positions regarding the range and significance of their work, as is generally expected from the development of scientific knowledge. In other words, systematics has definetely coped with the evolutionary paradigm on an overall basis, but specifically with the hierarchical organization of nature that can be comprehended soundly according to the phylogenetic/historical perspective. "*More than simply provide a caveat for the adaptationist program, the phylogenetic perspective has produced a battery of approaches and techniques that can be used to ask questions about the correlation between morphology and ecology while accounting for phylogenetic constraints.... Another major influence of integrating phylogeny is in greatly enhancing our understanding of the evolution of morphology and ecology*" (REILLY and WAINWRIGHT, 1997).

I expect it to be totally clear by now that it was not my aim to provide a manual on how to practically incorporate phylogenetic methods to planktological studies. Basic and comprehensive literature is already available to those interested in accomplishing this task (see WILEY, 1981; BROOKS and MCLENNAN, 1991; WAINWRIGHT and REILLY, 1997, for just a few examples). Actually, I also expect this paper to be read by those who work with the day-to-day traditional problems of plankton occurrence, abundance and diversity on ecological functional, structural and also morphological basis, problems that themselves deserve integrative solutions backed by substantial interpretative knowledge about the hierarchy of life.

The reader can easily access copious references in the planktological literature where the gaps between systematic and ecological focuses are evident. Copepods, for example, constitute the zoological group that probably includes the greatest number of individuals in the present biosphere (MARGALEF, 1983). Tons of descriptions of species and tentative descriptions of functional and structural aspects of the ecology of this group (specially if we speak of planktonic taxa) abound in the literature. However, no integration between these two types of information has been naturally pursued. I see the bridge between the above gaps in the form of consistent studies of the taxonomy and phylogeny of the numerous supraspecific taxa and species currently recognized, so that descriptive and analytical knowledge put together can yield potentially comprehensive hypotheses about patterns and processes of diversity.

CONCLUDING REMARKS

Effective concern about more integrated views uniting plankton, history and ecology are already on the run (see BAYLY, 1995, and COULBORNE *et al.*, 1998, for more recent examples). If one is to think in this way, much has still to be done in terms of producing phylogenetic and biogeographical knowledge, which is basically related to taxic evolution and to the ecology and evolution of the organisms themselves. I am convinced that this is the most adequate way to work with the diversity of planktonic life, since both its historical and ecological components can be deduced from phylogenetic studies. Therefore, the way to go in the planktological research, I believe, has to be opened to the discussion of the following problems: (1) the history (phylogeny) of any planktonic species has not been part of regular explanations of current functional or structural patterns of the ecology of the population to which it belongs; (2) the adaptationist approach to ecological problems emphasizes circular and descriptive explanations that apply to very specific contexts of the diversity issue; (3) planktological field work is severely limited by the tridimensional spatial nature of plankton, and this limitation is maximized by arbitrary criteria of sampling organisms and the resting on quantitative methodology to infer populational parameters; (4) methods of collecting plankton are now and will stay, for a long time to come, biasing and selective ones, restricting the reliability of functional and structural descriptions of plankton populations.

Ecology can only be descriptive if it is disconnected from a historical/phylogenetic perspective, and this is an inherent idiosyncrasy of this science. Planktology, practiced according the ecological perspective, has basically the same orientation. The field of planktology can proceed forever favouring this path, but its fate will always be of a first-level descriptive science. I hope that those who work hard both in the field and the laboratory trying to reveal the secrets of such a vast and diverse group of organisms like the planktonic ones will perceive that an individual cannot be understood apart from its history.

The critical meaning of this paper may appear preponderate throughout, and this has the explicit purpose of stimulating the discussion on the importance of systematics, through phylogenetic principles, as a generator of reasoning leading to comprehensive hypotheses on the occurrence, abundance and diversity of planktonic organisms.

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