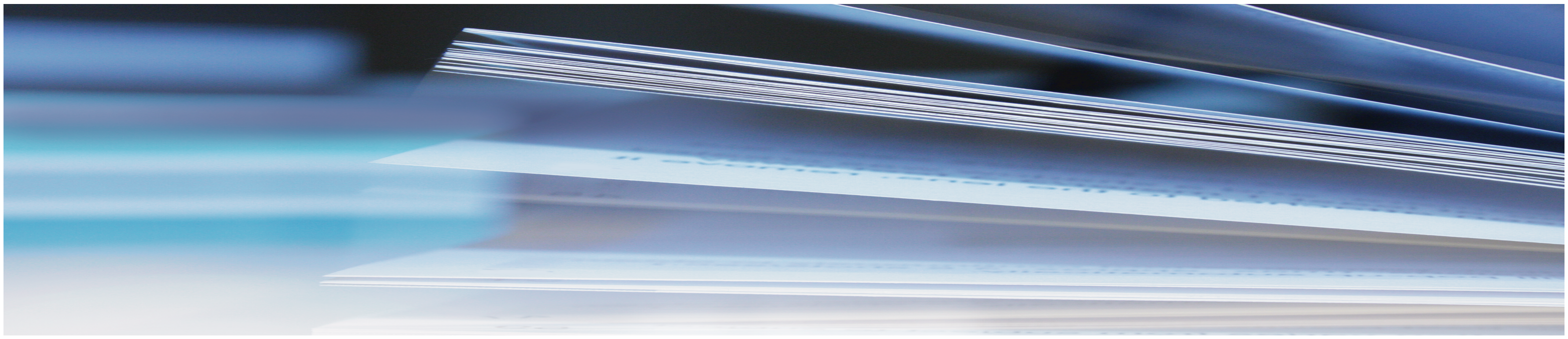

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ZOOPLANKTON:

Species Diversity, Distribution and Seasonal Dynamics

George Kehayias

MARINE BIOLOGY

ZOOPLANKTON

SPECIES DIVERSITY, DISTRIBUTION AND SEASONAL DYNAMICS

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GEORGE KEHAYIAS
EDITOR

nova publishers
New York

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PREFACE

Zooplankton organisms comprise very important elements of the structure and function of marine and freshwater ecosystems, not only as consumers of primary production grazing on algae, bacteria, protozoa and other invertebrates, but also as food items for juvenile stages of several fish species. Moreover, its strategic position in the aquatic ecosystems, as well as its sensitivity to both man-made and natural changes, makes zooplankton quite suitable for assessing alterations in the trophic dynamics and the ecological state of aquatic ecosystems related to changes in nutrient loading and climate. In this sense, changes in zooplankton abundance, species diversity and community composition can provide important indications of environmental change or disturbance. However, multiscale, spatial and temporal relationships between zooplankton variability and environmental heterogeneity are still not satisfactorily understood, due to the complexity of the different aquatic ecosystems (considering both biotic and abiotic elements), along with the global climate change. Thus, it is important to investigate the main factors that may govern the biology and ecology of these organisms, in order to have a better possibility to predict future changes, which might influence the biodiversity worldwide. The ambition of the present edition is to contribute to the understanding of the role of zooplankton by investigating ecological aspects such as the species diversity, their spatial distribution and seasonal dynamics in relation to the environmental influence in various aquatic ecosystems around the world.

Chapter 1 is dealing with the understanding of the role of zooplankton in transfer of pollutants through trophic food webs. Zooplankton is a group of organisms of key importance in regulating patterns and mechanisms through which matter, energy and pollutants are transferred from the base to the upper levels of food webs. Even if regarded as a homogeneous compartment, in reality zooplankton is composed by organisms which differ substantially one from each other, not only in their taxonomy, but also in body size, metabolic rates and ecological roles. While heterogeneity of the zooplankton compartment has been quite well documented in basic ecological studies, it is often overlooked in ecotoxicological ones, models in particular, which are usually mainly focused on sources and on top-levels of pollution patterns, the latter being directly related to human health. Such approach where intermediate steps are poorly considered, however, may result in detection of anomalous concentrations of toxicants in top-levels of the food chain, and in missing the essential links responsible for patterns and mechanisms of biomagnification. In the present chapter, the intension was to provide evidence for the need to incorporate into ecotoxicological studies, concepts and approaches developed in zooplankton ecology, not least the fact that zooplankton is made up by two hierarchical levels, or ecological roles, of primary and secondary consumers. By applying this perspective, it would be able to address mechanisms responsible for temporary mismatches and anomalies in concentration of pollutants, as a consequence of changes in space and time of these two hierarchical levels within the zooplankton community.

Red tides are remarkable phenomena implying sudden density increases (‘blooms’) of certain phytoplankton species and the subsequent toxin release from the phytoplankton cells, which can cause serious effects in the aquatic organisms. Chapter 2 focuses on mathematical modeling of plankton. First there is a review on few mathematical systems for plankton dynamics that have recently been proposed in the literature, in particular focusing on models for toxin producing phytoplankton. Then, new mechanisms are proposed that may possibly explain the toxin release as a phytoplankton reaction to zooplankton attacks, giving thus new material for testing to field marine biologists. In particular, three new models were introduced and compared in order to assess under what conditions red tides may occur. Specifically, the authors explore the possibility that phytoplankton specimens gather together for defense purposes, and then release the toxin through the surface of these agglomerates. The models suitably take into account this mechanism as well as the possible effects on zooplankton. A final discussion summarizes the results and compares the findings on the three models among themselves and with the earlier findings in the literature.

In Chapter 3, the authors evaluated the effect of inputs of nutrients, mainly nitrogen and phosphorus, on the structure of the zooplankton community, including diversity, evenness, dominance and richness, in a tropical reservoir

(Pampulha Reservoir) in the city of Belo Horizonte, Brazil. A series of thematic maps was used to describe the horizontal distribution of some variables and to examine whether areas with higher nutrient concentrations are associated with increases in dominance and decreases in diversity and species richness. The samples were taken on 15 September 2009 at 23 sampling stations, covering the entire reservoir. A spatial analysis showed that the species richness gradually decreased in those sites where increased nutrients and several highly opportunistic species increased in density along this same spatial gradient (such as *Thermocyclops decipiens*, *Metacyclops mendocinus* and *Brachionus calyciflorus*). Thematic maps showed that areas with higher nutrient concentrations were associated with increases in dominance and decreases in diversity and species richness. Finally, establishing the horizontal distribution patterns of zooplankton organisms in a reservoir allow the authors to perform a detailed ecological zonation of the water body and one of the most interesting applications of this zonation is the identification of ecological gradients related to pollution sources.

Chapter 4 provides elements on the community structure, the spatial and seasonal variation and the relation of zooplankton to environmental parameters in five Greek lakes through an extensive investigation between 2003 and 2010. In particular, the studies were conducted in four natural lakes (Trichonis, Amvrakia, Lysimachia and Ozeros) and one reservoir (Stratos). Zooplankton surveys of 12 to 24 months were conducted in all ecosystems, while at the same time the most important physicochemical parameters were recorded. The number of species in the five lakes varied between 25 (Lake Ozeros) and 36 (Lake Lysimachia). The general similarities in species composition in the five lakes can be attributed to their common geological origin, while differences among them are ought either to geographical isolation, to the particular water chemistry, or to their trophic state. The group of copepods, and especially the calanoid *Eudiaptomus drieschi*, dominated the zooplankton community in the oligotrophic Trichonis Lake, the oligo-mesotrophic Amvrakia Lake and the meso- eutrophic Ozeros Lake. Instead, the group of rotifers dominated in the eutrophic Lysimachia Lake and in Stratos reservoir. The cladoceran species presented clear seasonal dominance succession patterns, with *Bosmina longirostris* and *Diaphanosoma orghidani* occupying the greatest percentage in winter and summer months, respectively. The larvae of the mollusk *Dreissena blanci* were important constituent on the zooplankton community in most of the lakes, except Lysimachia. In the deep lakes Trichonis and Amvrakia, the higher zooplankton density was recorded in the surface 0–20 m layer and was decreasing with depth, while small numbers of zooplankton specimens were found also in the hypoxic/anoxic hypolimnion of the latter lake. The vertical separation of the numerically most important species of crustaceans and rotifers is attributed possibly to the reduction of intra- and inter-specific competition. Temperature was the most important environmental parameter for most of the species variation, while other elements like dissolved oxygen, water level fluctuation, conductivity, chlorophyll-a and nutrients concentration played also important role in the zooplankton spatial and temporal distribution in the five lakes.

Chapter 5 is dealing with a zooplankton community in a particular freshwater ecosystem such is the cooling reservoir of the Beloyarskaya Nuclear Power Station (BNPS) in the Middle Urals. In particular, this chapter reports the results of an extended investigation (1986–2011) on the state of the zooplankton complex, focusing on species characteristics and their capacity to accumulate radionuclides and microelements from the water of this reservoir. The zooplankton species composition, abundance and biomass were investigated in four zones of the reservoir: the heated water discharge zone, the discharge and water intake channels, the control region and the central water area. In the observation zones the investigated parameters were different. Thus, in Teplyi Bay and in the discharge channel adjacent to the power station the abundance and biomass of zooplankton were much lower after its entrance through the cooling system of the station. The analysis of mortality among the predominant species evidenced of the greater sensitivity to injuring factors of copepods in comparison to cladocerans. The main attention was paid to the water discharge channel through which low-radioactive water was discharged into the cooling reservoir. The quantity of radioactive pollutants entering the cooling reservoir together with zooplankton was estimated. The investigation of the accumulation levels of ^{90}Sr and ^{137}Cs in the zooplankton, as well as in other hydrobionts and in the sediment, showed considerably higher accumulation coefficients in the case of phyto- and zooplankton in comparison to fish species, mollusks and the sediment. The accumulation coefficients of 70 chemical elements in the zooplankton ranged from 10^2 to 10^7. A significant positive correlation between the concentrations of chemical elements in zooplankton and the water medium indicated that zooplankton generally reflected the chemical composition of its habitat and responds quickly to changes in the chemical composition of the water. Thus, zooplankton can be considered as a highly sensitive biogeochemical indicator of water pollution with heavy metals and radionuclides.

Some aspects of the spatio-temporal dynamics of certain zooplankton groups (Cladocera, Copepoda) in the Danube River were investigated in Chapter 6. Despite rapidly growing insights into zooplankton spatio-temporal dynamics in lotic environments, syntheses of prior case studies have not yet been given much effort. Thus, in this chapter the authors aimed to assemble the pieces of some of their previous case studies performed in the Danube River near Budapest and to put all those findings into a more coherent framework. It is pointed that these studies do not cover the full range of dimensions affecting microcrustacean dynamics and diversity in the river, but rather demonstrate a representative subset of spatio-temporal aspects of microcrustacean dynamics. The chapter discusses the horizontal variation of crustacean zooplankton abundance across the river channel and demonstrates that different taxonomic and life-history clusters exhibit various patterns. The complex interactive effects of the flow regime with nutrient inputs on riverine zooplankton are discussed on the example of the waste water discharges entering the river at Budapest. The short-term variation of microcrustacean dynamics on the basis of samples collected on a daily basis was demonstrated. This sampling design allowed for testing the effects of sampling effort and sampling frequency on the estimation of the composition and abundance of microcrustacean assemblages in a side arm of the river. Furthermore, the authors discuss the possible effects of climate change on microcrustacean dynamics by means of a simple simulation model. Finally, a list of recommendations is given as how to improve the understanding in this evergreen field of limnology.

Chapter 7 is dealing with the abundance and trophic position of gelatinous zooplankton in a productive marine area such as the Namibian upwelling region in the west coast of South Africa. In this investigation the term “gelatinous zooplankton” is used for Coelenterata only, such as Cnidaria and Ctenophora. These carnivorous gelatinous organisms mainly feeding on zooplankton, fish larvae and small fishes and are considered as end members of the food web as they are only eaten by a few species like some fishes, other cnidarians and sea turtles. Since the 1970’s the abundance of large gelatinous zooplankton increased in the northern Benguela probably due to overfishing and/or climate change. Although several papers about the taxonomy and ecology of gelatinous zooplankton in the northern Benguela region exist, data on the vertical and horizontal distribution of small Medusae and their role in food web dynamics are still limited. Only the distributions of large jellyfish like *Chrysaora* spp. and *Aequorea* spp. were examined in several studies, as well as the effects of advective processes on gelatinous zooplankton. Thus, this chapter presents data about the onshore/offshore and vertical distribution as well as the taxonomical composition of these organisms in the northern Benguela Current System. Furthermore, it provides insights into their trophic position using a stable isotope analysis. Samples were taken with a multiple opening and closing net in March 2008 and in December 2009 along a transect off Walvis Bay (Namibia) from the shelf towards the open ocean. Additional samples were taken with different types of gears at several stations in the northern Benguela for stable carbon and nitrogen isotope analyses in December 2009. The taxonomical composition of all groups revealed an inshore/offshore gradient with higher diversity offshore. Medusae and Siphonophora were treated separately since Siphonophora live in colonies which break into pieces when caught by nets. Medusae were generally smaller in size at the offshore station, whereas no size distribution gradient was found for the single individuals of Siphonophora. The numerical abundance of both Medusae and Siphonophora parts were variable along the onshore-offshore transect. Within the Medusae, Trachymedusae dominated the offshore system and Leptomedusae the inshore system. Within the Siphonophora, the system was dominated by Diphyidae in offshore and costal waters and on the inner shelf in 2008 and by Agalmatidae at the slope, shelf-break, outer shelf and inner shelf in 2009. A heterotrophic level of two and higher was calculated for the gelatinous zooplankton.

Finally, Chapter 8 is dealing with the seasonal dynamics of a zooplankton community in a particular environment such as a man-made solar saltern (Sfax solar saltern in Tunisia), as well as with the interrelation with the environmental parameters. Sfax solar saltern is an artificial system formed of interconnecting ponds of different salinity extending over an area of about 1500 ha, along the coast to the south of the town of Sfax (Tunisia) over a distance of 12 km. In this area, four ponds of increasing salinity (A1: 41 psu; A5: 46 psu; A16: 67 psu; and C31: 77 psu) were selected to be the study sites for the investigation of the seasonal distribution of zooplankton abundance, along with the environmental factors. Measurements were taken monthly, during a year (September 2007 to August 2008). A total of 21 zooplankton taxa, belonging to copepoda (17 species), rotifera (3 species), cladocera (1 species) and other zooplankters, were identified. Copepoda was the dominant group in all sampling ponds and accounted for 65% of the total zooplankton density in the Sfax solar saltern. The results showed that salinity differ significantly among the four ponds and that the zooplankton abundance decreased with increasing salinity of the ponds. However, the highest density of total zooplankton (70.76×10^4 ind.m^{-3}) the author recorded in the first pond

A1. Differences in the density of zooplankton were found between ponds. The density of total zooplankton as well as of copepods and rotifers were negatively correlated with salinity, while positively correlated with total phosphorus. In conclusion, in this particular ecosystem, spatial and temporal variations in zooplankton abundance can be related to the environmental variability, while salinity seems to play the major role in determining spatial and temporal patterns.

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Chapter 1

UNDERSTANDING THE ROLE OF ZOOPLANKTON IN TRANSFER OF POLLUTANTS THROUGH TROPHIC FOOD WEBS

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ABSTRACT

Zooplankton is a group of organisms of key importance in regulating patterns and mechanisms through which matter, energy and pollutants are transferred from the base to the upper levels of food webs. Even if regarded as a homogeneous compartment, in reality zooplankton is composed by organisms which differ substantially one from each other, not only in their taxonomy, but also in body size, metabolic rates and ecological roles. While heterogeneity of the zooplankton compartment has been quite well documented in basic ecological studies, it is often overlooked in ecotoxicological ones, models in particular, which are usually mainly focused on sources and on top-levels of pollution patterns, the latter being directly related to human health. Such approach where intermediate steps are poorly considered, however, may result in detection of anomalous concentrations of toxicants in top-levels of the

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food chain, and in missing the essential links responsible for patterns and mechanisms of biomagnification. In the present chapter, we provide evidence for the need to incorporate into ecotoxicological studies, concepts and approaches developed in zooplankton ecology, not least the fact that zooplankton is made up by two hierarchical levels, or ecological roles, of primary and secondary consumers. By applying this perspective, we are able to address mechanisms responsible for temporary mismatches and anomalies in concentration of pollutants, as a consequence of changes in space and time of these two hierarchical levels within the zooplankton community.

MAIN CHARACTERISTICS OF ZOOPLANKTON AND THE FRESHWATER FOOD-WEB

Heterogeneous by definition is the nature of zooplankton, the term itself referring to a life habit- that of being passively transported through the water medium – rather than to taxonomic affiliation and e.g. ecological role. To share a common status of being passively transported by large scale water movements are, in addition to zooplankton, both, phytoplankton, and the so-called mixoplankton, i.e. plankton organisms able to switch from auto- to heterotrophy.

In its ordinary meaning, zoo-plankton designates animal organisms living in the water column, which are collected with a plankton net (thereafter also known as “net zooplankton”), whose mesh size allows for retaining organisms swimming in the water column within a certain size range. Using nets implies filtering water to get enough material to represent composition and relative proportions of variety of organisms composing the zooplankton community (de Bernardi, 1984). Using nets also allows for integrating horizontal and vertical heterogeneity in distribution of organisms composing the zooplankton. Finest nets used for sampling zooplankton are generally of 50 µm porosity; finer nets soon becoming clogged by phytoplankton algal cells during filtration, thus making it difficult to separate zoo- from phyto- components of plankton.

Zooplankton nets therefore provide insight into a specific size fraction of the zooplankton from which, the so-called microzooplankton (size between 20-200 µm, including Protozoa, ciliates, Rotifera) is excluded in its smaller size fraction. Being ca. one order of magnitude more abundant than net zooplankton, small microzooplankton is usually collected and analyzed by the same methods used for phytoplankton (*i.e.* with Van Dorn bottles), which do not imply water filtration and concentration of organisms present in the filtered water volume. A wide range of mesh sizes allows for collecting net zooplankton in a wide range of body sizes, from small-sized monogonont rotifers (e.g. *Keratella cochlearis*, body length as small as ca. 80 µm) to adult copepods and cladocerans whose body lengths reach centimetres, through naupliar and copepodite developmental stages of copepods.

Organisms composing net zooplankton are diverse for taxonomic affiliation, ontogeny and body size. While zooplankton taxa richness and diversity are useful tracers of degree of maturity and level of developmental history of aquatic environments, size structure, particularly of the zooplankton, allows for understanding the degree of impact of environmental cues, which is in turn essential for forecasting reaction time of aquatic ecosystems in response to perturbations.

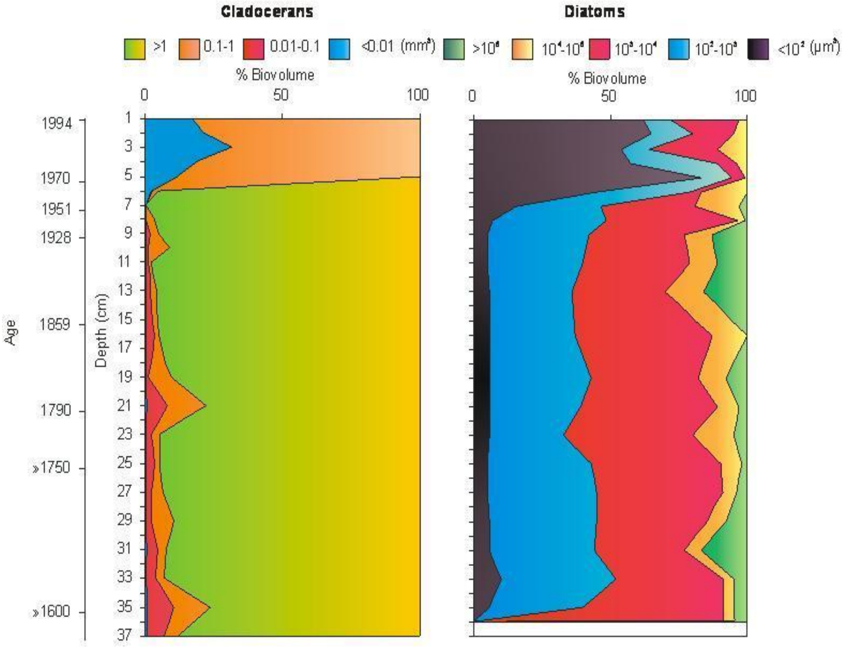

Figure 1. Temporal variations in size structure of cladoceran and fossil diatom assemblages in a sediment core collected in Lake Orta. Shift towards smaller sized was detected with onset of pollution (modified from Cattaneo et al., 1998).

Size-specificity is, in fact, one of the major traits governing biotic and abiotic interactions within and between the zooplankton (Peters, 1983). Fast-reproducing, small-sized organisms are characterized by a faster response to environmental cues than larger-sized ones. Furthermore, they tend to show larger variations in abundance than larger-sized ones. The ability to fast grow in numbers is, in turn, responsible for being small-sized zooplankters, promoters of re-colonization of environments restored after pollution, pioneering further successful establishment of larger-sized ones (Figure 1; e.g. Cattaneo et al., 1998).

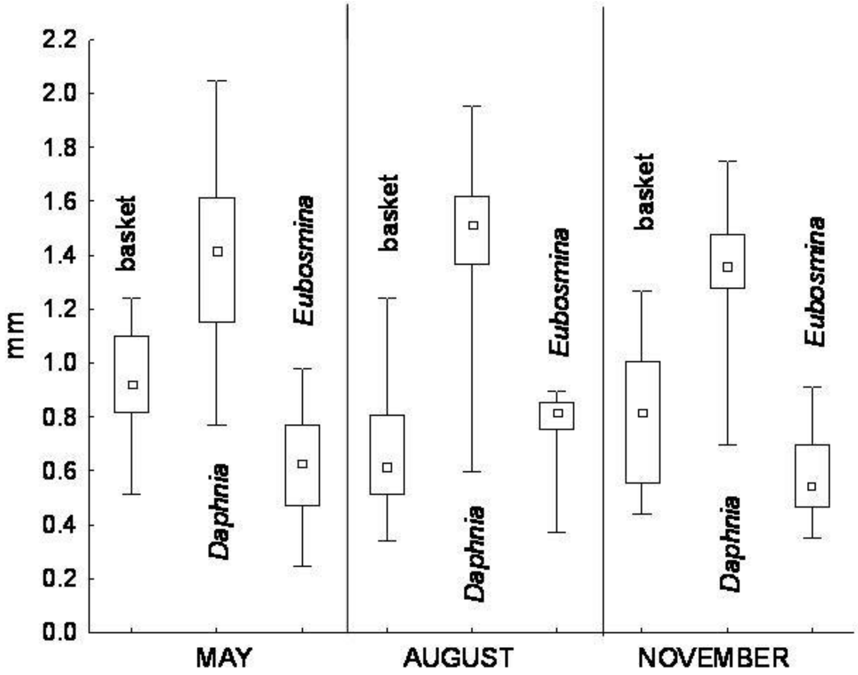

Figure 2. Seasonal changes in *Leptodora's* feeding basket opening diameter and in body length of cladoceran prey available in the water column of lago d'Iseo, Italy (modified from: Beluzzi et al., 2013).

Between- and within-zooplankton biotic interactions are also size-specific. From body size depends the size spectra of edible food of filter-feeding Cladocera (commonly known as "water-fleas"). Food particles are retained by these organisms through filter combs bared by thoracic limbs, in a range of sizes that is constrained by the distance between the setae forming the combs (Geller and Müller, 1981). Such distance tends to increase with body size (although being large *Daphnia magna* an exception), thus allowing larger species/specimens for retaining increasingly larger food particles, and smaller ones, to exploit also smaller food particles, such as bacteria. Seasonal succession of filter feeding cladoceran species can be interpreted as a succession from coarse-mesh filter-feeders to fine-mesh filter-feeders. Not only food particle size, but also filtration rate largely depends on body size (Porter et al., 1983).

Common exploitation of food sources is, in turn, responsible for a strong competition between filter-feeders overlapping in body size (Brooks and Dodson, 1965). Severe competition between closely related species is predicted to drive extinction of the less efficient, a prediction that is, in fact, disproved by the great diversity of plankton communities (Hutchinson's paradox of plankton in "Homage to Santa Rosalia or why do we have so many species" Hutchinson, 1961). What we may regard as severe competition under laboratory and mesocosm experiments can be, in fact, attenuated under environmental conditions with which species have interacted in the field. Establishment of species in a given environment is a long process of adaptation to physical and chemical conditions which, along the way, are changed by living organisms themselves (de Bernardi, 1981). During the establishment of species, competition can be released by means of e.g. spatial and temporal separation in vertically and horizontally structured aquatic environment (Bossone and Tonolli, 1954 in Hutchinson, 1967). Factors leading to release in competition pressure include predation.

Zooplankton includes most favourite prey of fish which, at least during early life stages, substantially feed on them. Predation by fish and vertebrates is, in general, visual, therefore depending on prey size and visibility (de Bernardi et al., 1987). Transparent body of crustacean zooplankters becomes more visible to predators when e.g. colourful eggs are produced and released by mature females, thus making fish predation not only size-, but also developmental stage-specific. In turn, ovigerous females are able to cope with fish predation pressure by migrating into dark, deep, water layers during the day, returning to upper water layers when light is attenuated. While being traditionally restricted to fish and vertebrates, visual predation has been found also in the case of the pelagic cladoceran species *Bythotrephes longimanus* (the "spiny water flea"), as well as the Onychopod cladoceran *Polyphemus pediculus* (Brooks and Dodson, 1965), whose compound eye was proved to be useful also for visually detecting prey. Similarly to that exerted by planktivorous fish, *Bythotrephes* predation is more intense under light conditions than in the dark (Muirhead and Sprules, 2003; Pangle and Peacor, 2009).

Size of edible prey is in turn constrained by predator's body size, the latter being also related, in given environment and time, to developmental stage, from which swimming rate also depends (Manca et al., 2008). Among *Bythotrephes*' favourite prey is *Daphnia,* which is also among the most preferred prey of planktivorous fish, therefore suggesting a competition between *Bythotrephes* and fish for medium-sized *Daphnia,* including ovigerous females (Manca et al., 2000).

Size-specificity in prey selection also characterizes another predatory cladoceran, *Leptodora kindtii* (Cladocera Haplopoda). This carnivorous cladoceran swims continuously through the water column, capturing prey by means of five pairs of thoracic appendages spread to form a feeding basket (Manca and Comoli, 1995; Herzig and Auer, 1990; Vogt et al., 2013). Among prey encountered directly in front by a free-swimming *Leptodora*, only those able to fit into basket opening can be captured. As basket diameter increases with animal body length, size selection of prey depends on *Leptodora*'s body size (Figure 2.). The same is for other zooplankton invertebrate predators, such as *Chaoborus* larvae, the size of their edible prey depending on larval developmental stage and on the size of mandibles used to process the prey.

When planktivorous fish are present, size structure of predatory zooplankton is mainly controlled by fish predation pressure. Zooplanktivorous fish are very selective for the prey: they prefer *Bythotrephes* over *Daphnia* and the latter over cyclopoids (de Bernardi et al., 1987; Figure 3). Preference for *Bythotrephes* is so strong that the first record of the species, from Bodensee, was not of intact specimens from open-water zooplankton, but from *Bythotrephes* body remains in the stomach of a whitefish, *Coregonus wartmanni* (in Sars, 1861). As fish tend to select large individuals within the population, the extent to which *Bythotrephes* is preyed by zooplanktivorous fish can be inferred by changes in its maximum body size. Such changes result from body (plus tail spine) length (Manca and Comoli, 2000; Burkhardt, 1994; Figure 4). Tail spine length, in turn, influences swimming rate, as longer-tailed individuals are faster than shorter-tailed ones.

Similarly, impact of fish predation on *Daphnia* both, across and within lakes, can be detected through *Daphnia* maximum body length, as it tends to decrease with fish predation pressure. Population mean body length is not as informative as maximum body length, being influenced by food conditions and ambient temperature. Diluted food conditions and cool temperatures favour increased body sizes, while concentrated food conditions and increasing temperatures promotes smaller body sizes. Similarly, removal from *Daphnia* population of large ovigerous females by planktivorous fish results in decreased minimum size of primiparae (Manca and Galli Tognota, 1993; Lampert, 2011)

Other than standing stock biomass and density, size-specific population traits and demographic parameters of key zooplankton taxa allow for detecting patterns and driving mechanisms through which matter, energy and pollutants flow through the environment to reach upper levels of the food web (e.g. piscivores, by means of planktivores and human exploiters). Depending on zooplankton organisms present at a given time and in a given space, number of steps through which matter, energy and pollutants are conveyed to upper levels of the food web varies, also after changes in contribution of primary and secondary consumers within the zooplankton.

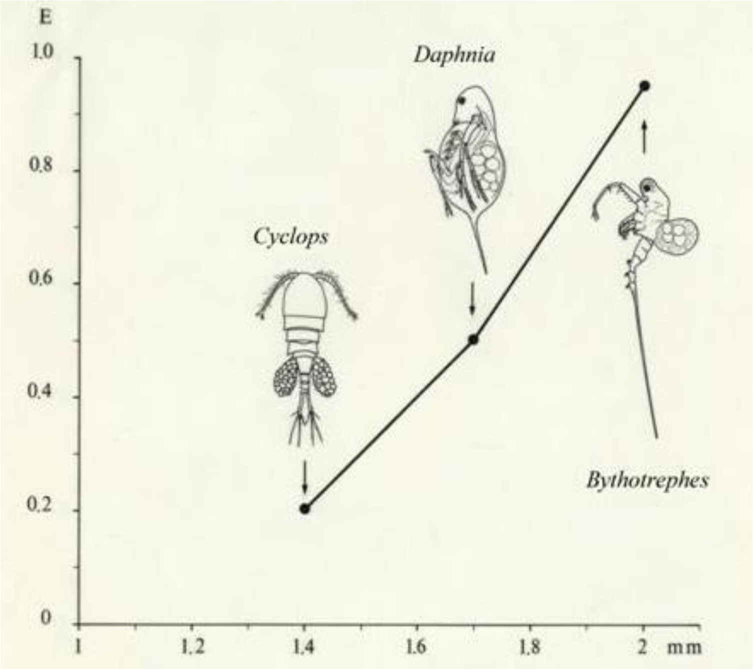

Figure 3. Selection (E, electivity index, according to Ivlev) of planktivorous fish on zooplankton (from: de Bernardi et al., 1987).

In temperate lakes, similarly to what observed in marine plankton, seasonal changes in standing stock biomass and population density of the zooplankton can be summarized as a succession of three main phases: an initial phase of increase leading to primary consumers' population peak following increase in phytoplankton biomass, which promoted enhanced food conditions; a second phase, during which predatory zooplankters (secondary consumers within the zooplankton) are able to grow, selectively exploiting zooplankton primary consumers, substantially contributing to their decline; a third phase, during which increase in primary consumers is consequent to a second phytoplankton peak (Cognetti et al., 2008).

Migration of fish from the littoral environment, where they recover for spawning and reproducing during winter, into the pelagic zone has been found synchronized with the initial increase in zooplankton primary consumers, e.g. in a deep, large, temperate lake (Lago Maggiore, Italy; Visconti et al., 2013). During this period, *Daphnia*, the main filter-feeder soon became preferred prey of zooplanktivorous fish, the latter therefore acting as secondary consumers (two steps higher than primary producers). Later in the season, when predatory cladocerans, e.g. *Bythotrephes* and *Leptodora* grew and planktivorous fish shifted towards them, the system gained a third step in food web.

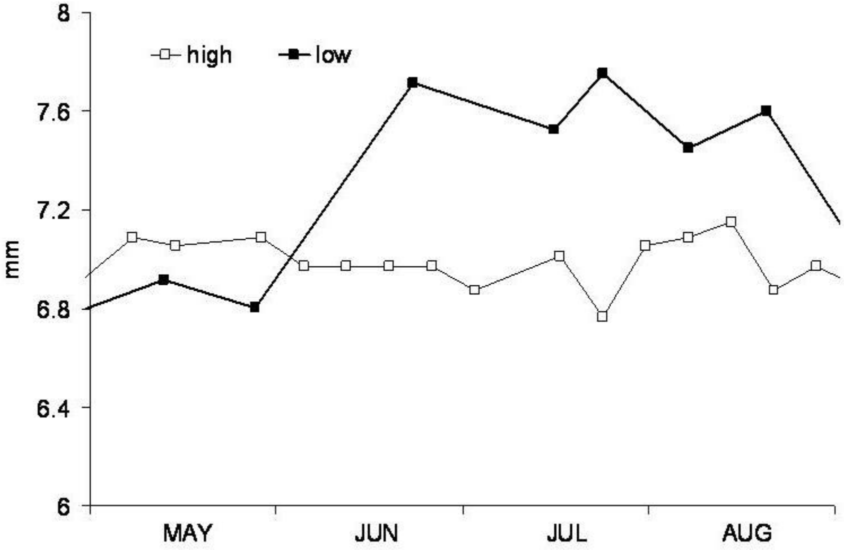

Figure 4. Comparison of *Bythotrephes* maximum body size (length, mm) attained in Lago Maggiore, in two years during which predation pressure was different.

An easy and relatively well applied method for investigating changes in food web is carbon and nitrogen stable isotope analysis (C, N Stable Isotope Analysis - SIA). By this method, food sources (e.g. littoral vs. pelagic, deep vs. shallow) can be clearly identified in a system, as well as the time-specific contribution of organisms to food webs. The method was originally applied to marine environments and to fish in particular, not least for fingerprinting their origin. Also recently, it has been increasingly applied in freshwater environments, not only on fish or other organisms of direct human consumption, but also on those which sustain their production and growth, thus allowing for a more reliable reconstruction of the food web (Perga and Gerdeaux, 2006). SIA is applied to investigate ecosystems in the making, but also for predicting, by means of organism nitrogen isotopic signature, time and space specific trophic position, from which, among the others, biomagnification depends (Hobson et al., 2002; Galassi et al., 2012; Piscia et al., 2013).

Often restricted to one or few time spots, SIA is increasingly applied to investigate seasonal dynamics in lakes. Interest in applying SIA seasonally is consequent to awareness of being aquatic environments highly variable in time, an attribute deriving from the intrinsic nature of the aquatic medium. Seasonal succession is increasingly regarded as not only taxa-, but also ecologically- and functionally-informative. While the increasing exploitation of molecular techniques allow for understanding the taxonomic diversity at a fine resolution level, “operational” (*sensu* Moss et al., 2009) approaches are to be implemented in view of predicting impact and reversibility of impact of changes at global and regional scales. Stable Isotope Analysis may be regarded as a molecular approach (Strayer, 2010) used as a functional approach (i.e. “operational”, *sensu* Moss et al., 2009) (Boggio et al., 2013). Carbon and nitrogen stable isotope analyses have been recently applied to Lake Maggiore monitoring, to investigate seasonal changes in both, taxa-specific crustacean zooplankton and main planktivorous fish, for highlighting changes in ecological roles and exploitation of carbon sources.

Investigating seasonal changes in carbon and nitrogen isotopic signature of pelagic zooplankton taxa in Lake Maggiore, it was found that during winter, when whitefish and shad were feeding in the littoral environment, predatory zooplankters like *Bythotrephes* and cyclopoids’ adults played a vicariant role of the fish, with the highest level of nitrogen enrichment with respect to baseline. With migration of fish into the pelagic zone, in spring-early summer, nitrogen signatures of both, predatory and filter feeding planktonic cladocerans became least enriched. A return towards a higher level of enrichment was observed later on. Stepwise enrichment was also smaller when fish-, in addition to infrazooplankton-predation, was detected in the open water. A similar pattern was found in other deep, subalpine lakes.

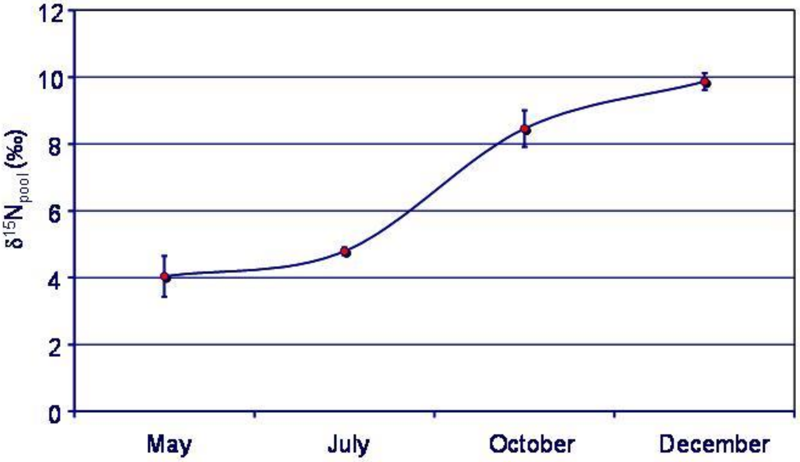

Figure 5. Seasonal changes in nitrogen isotopic signature of pool zooplankton (>450 µm).

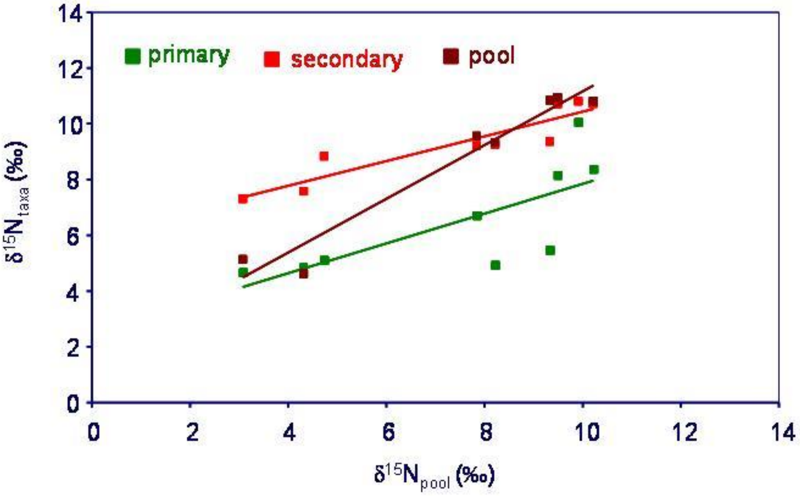

Figure 6. Seasonal changes in nitrogen isotopic signatures of zooplankton in different samples. Pool zooplankton samples change seasonally, being in spring (left side) mainly influenced by primary, and in fall (right side) by secondary, consumers, the latter being more enriched in ^{15}N than the former.

Isotopic signatures of mixed zooplankton in a size fraction edible for the fish were found to vary seasonally, from more ^{15}N enriched values in winter and fall to less ^{15}N enriched values in spring and early summer. Changes observed were at least partly related to relative contribution of primary vs. secondary zooplankton consumers; basically, under prevalence of primary consumers lower levels of nitrogen enrichment were measured, while an increase in contribution of carnivorous taxa to total zooplankton biomass was related to a higher level of enrichment in nitrogen isotopic signature (Figures 5 and 6).

ZOOPLANKTON AS A MEANS OF TRANSPORT OF POLLUTANTS

In a pelagic environment primary producers such as phytoplankton traditionally have been considered as the initial step for transport of persistent organic pollutants (POPs) into food webs. However, the capacity of uptake of zooplankton is undoubtedly a key route for POPs transportation via the food chain. At a glance, zooplankton community seems to have a homogeneous nature and it seems that the relationships among different organisms and their roles in aquatic environments are particularly streamlined; therefore zooplankton can be easily used as a model for the representation of more complex ecosystems. In reality, as already underlined, zooplankton is made up of organisms which differ substantially one from each other, not only in their taxonomy, but also in body size, metabolic rates and ecological roles. While heterogeneity of the zooplankton compartment has been quite well documented in basic ecological studies, the implications from an ecotoxicological point of view are still a subject matter.

The contamination of a certain organism at any level of the food chain is called bioaccumulation. Bioaccumulation is the process of concentration of contaminants into biota which reach higher levels than the medium in which organisms live (Figure 7). The process of bioaccumulation is particularly complex and the implementation via-food, known as biomagnification, can cause additional significant bioaccumulation, resulting in an increase in chemical concentration with increasing trophic level in food chains (i.e. trophic magnification) (Gobas et al., 1988; Suedel et al., 1994). Mechanisms and way for bioaccumulation in fish are quite well-known; fish can bioaccumulate organic chemicals from the food they eat and from their intake of particulate in water and in sediments onto which the chemicals have adsorbed (Figure 8). In many such cases the contaminants are not metabolized by the fish, the substance simply accumulates in the fatty tissue of the fish where its concentration increases. As a result concentrations in fish can become 100,000 times the concentrations measured in the water depending on the chemical-physical characteristics of the pollutant (Mackay, 1982; Mackay and Fraser, 2000). The bioaccumulation phenomenon of hydrophobic chemicals can be predicted by taking advantage of the reliable relationship between the octanol-water partition coefficient (K_{ow}). Through the use of mathematical models (Gobas, 1993) predictions of contaminant levels in fish can be obtained; however environmental systems and the variability of the composition of the trophic webs are so complex that not always the gathered information is reliable. Little is still known on the role of the transfer of contaminants from the lowest trophic levels in lakes. At these levels, the uptake of contaminants is not completely clarified and the variability of field-measured contaminant concentrations makes the valuation of levels reached at the higher trophic levels uncertain (Glaser and Connolly, 1995). Therefore, zooplankton is still rarely included in investigation of the seasonal patterns of contamination in relation to its composition and behavior. Only a few monitoring campaigns have included this important component of the pelagic food web, probably because its role in the biomagnification process is not fully understood (Day, 1990; Berglund et al., 2001).

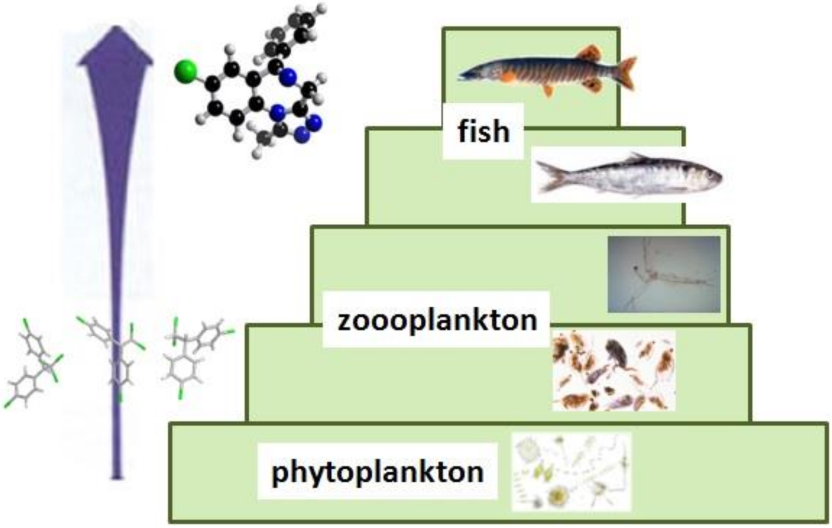

Figure 7. Pelagic trophic chain and implementation concentrations of contaminants.

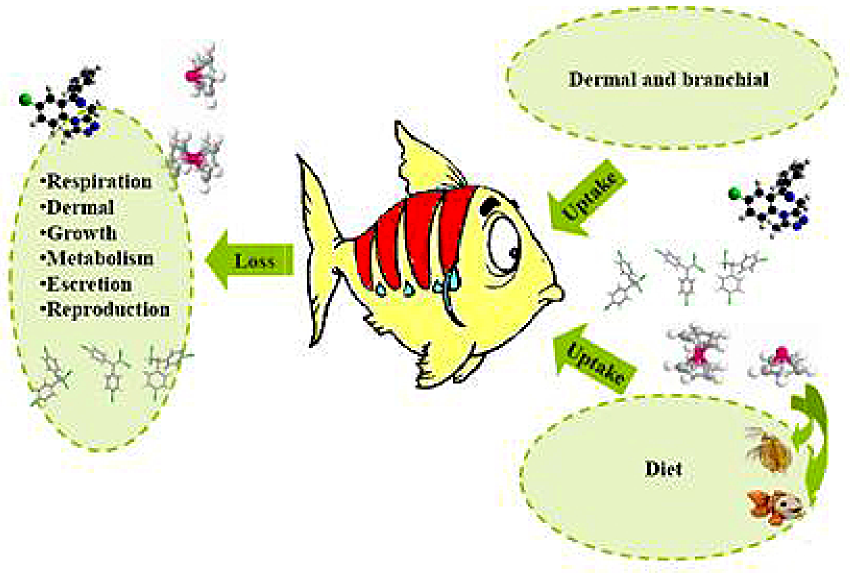

Figure 8. Uptake and loss of contaminants by fish.

A monitoring project (CIPAIS project) aimed at identifying mechanisms through which persistent organic pollutants (DDTs in particular) transfer through the pelagic food web, has been carried out for around the last fifteen years on Lake Maggiore, Northern Italy. Beginning in the 1990s, DDT pollution originating from industrial activity was discovered in the lake which is one of the largest (surface area, 212 km^2) and deepest (maximum depth, 372 m) lakes in Italy. This contamination posed serious threats to both top predators and fishery activities (Bettinetti et al., 2005). The monitoring project, initially on contamination of fish, after DDT fish pollution becoming evident, focused on the zooplankton, as an early warning system of persistent organic pollutants in deep lakes. Stable isotope analyses of zooplankton, applied to investigate the transfer of pollutants to planktivorous fish, seem to be a successful mean of monitoring too. As a result, the combination of the two way of investigation seems to be particularly successful in predicting the contamination of a freshwater environment (Bettinetti et al., 2012) Zooplankton accumulate organochlorine compounds more rapidly than fish and it is expected to respond much faster than their predators to fluctuations of pollutants occurring in the water column (Bettinetti et al., 2010). Larsson (1989) observed the same extent of the atmospheric deposition of PCBs in the uptake of zooplankton from a pond in southern Sweden; the prompt response of the zooplankton results from their comparatively short life span and their ability to equilibrate very quickly with water (Larsson, 1989). Zooplankton reacts much more promptly than fish to OC concentration changes in the water column, caused by hydrological events, such as lake circulation or thermal stratification (Bettinetti et al., 2010). These attributes suggest that zooplankton as component of the pelagic food web may be used as an early warning tool of a possible contamination.

An important aspect to be taken into account for future use of zooplankton as biomonitoring tool is related to the trophic level of this important community. Models generally consider zooplankton as trophic level 2 (Connolly and Pedersen, 1988; Campfens and Mackay, 1997) without taking into account complexities including species-specific differences in life cycles, size and feeding habits. Since, as mentioned, the relative proportion of species can change greatly during the year, especially in lakes of temperate climates, carnivorous species can represent a significant portion of zooplankton community biomass during certain time periods (Visconti and Manca, 2011), thus violating the assumption that the entire community can be placed at the level 2.

CONCLUSION

Since most of the available studies have used food web models validated with data without considering the lowest trophic levels concentrations with proper details, in this chapter we have underlined the main characteristics of zooplankton community, pointing out the importance of taking into account these organisms in ecotoxicological investigations: zooplankton plays a key ecological role and it should be considered when assessing the risk for the ecosystems. Therefore, more studies should be dedicated to the implementation of understanding the roles of predators and herbivores within the group of zooplankton and in the pelagic freshwater food-web.

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Chapter 2

A COMPARISON OF SEVERAL PLANKTON MODELS FOR RED TIDES

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Abstract

In this chapter we first review a few mathematical systems for plankton dynamics that have recently been proposed in the literature, in particular focusing on models for toxin producing phytoplankton. Like in theoretical physics, we then propose new mechanisms that may possibly explain the toxin release as a phytoplankton reaction to zooplankton attacks, giving thus new material for testing to field marine biologists. In particular we introduce three new models and compare them in order to assess under what conditions red tides may occur. Specifically, we explore the possibility that phytoplanktons gather together for defense purposes, and then release the poison through the surface of these agglomerates. The models suitably take into account this mechanism as well as the possible effects on zooplankton.

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AMS Subject Classification: 92D25, 92D40

1. Introduction

The role of mathematical biology should be to provide theoretical frameworks for the field biologists to test, as in a certain sense do theoretical physicists, when they construct theories that subsequently need to be verified by suitable experiments. Such a concept was expounded during the plenary talk given by L. Ginzburg at the Alcalá AICME03 meeting in 2003, presenting the then forthcoming book [17].

Here our aim is to move along these lines, by proposing a theoretical framework to provide ideas for the setting up of suitable experiments for their possible validation or rejection. In fact, tests perfomed by field ecologists or applied scientists need in general to have a theoretical guideline in their support.

In general there is mutual fecundity between the theoretical and applied sciences, that results to be beneficial to both. In this context the formulation of models has therefore always been fundamental in the history of science, whether consciously recognized or not. For instance, astronomical observations on light deflection during a solar eclipse to verify the predictions of general relativity are well known. On the other hand, occasional empirical discoveries have led afterwards to the formulation of comprehensive theories of which the discovered facts are just a particular issue. The early experiments of Faraday on electricity in the nineteen century have been followed later on by the formulation of vector calculs and field theory; in the second half of that century they led to mathematical developments like quaternionic theory and Clifford algebras.

In the fairly recent history of science, an example of this way of proceeding can be found in biomedical research. It is provided by a paper that proposed the way antibody production occurs in the human body. The original theory [21] was modified in the late fifties of the past century [7] just on a speculative basis. Only many years later the modification was assessed in laboratory experiments, and is now accepted by the scientific community. A nice historical account of these facts, together with a reprint of the original articles is contained in [20].

In this Chapter, we focus on mathematical modelling of plankton. This research area aroused the interest of the scientific community since about two decades. We organize the exposition by first reviewing a number of recent contributions in the next Section. The brief Section 3 contains the discussion of the basic assumptions in the new models. These are illustrated in the subsequent three Sections. A final discussion summarizes the results and compares the findings on the three models among themselves and with the earlier findings in the literature.

2. Literature Background

Plankton lies at the basic trophic level of the entire aquatic food chain and therefore of all the food webs on Earth. In mathematical biology plankton research has become relevant since the seminal works of the last decade of the past century, [4, 14–16, 24, 30].

Before proceeding to introduce the new models, in this Section we present a brief review of some more recent contributions in this field, that are related to the models we will introduce later on.

In [10], a very general model composed of two plankton populations, namely zooplankton Z and toxic phytoplankton P, is considered.

$$\begin{cases} \dot{P} = rP_1\left(1 - \dfrac{P}{K}\right) - \alpha f(P) Z \\ \dot{Z} = \beta f(P) Z - \mu Z - \theta g(P) Z\,. \end{cases} \tag{1}$$

Several functional forms are used in place of the responses $f(P)$ and $g(P)$. The forms considered are the Holling type I, II and III, namely

$$h(P) = P, \quad h(P) = \frac{P}{\gamma + P}, \quad h(P) = \frac{P^2}{\gamma^2 + P^2},$$

where $h(P)$ represents either $f(P)$ or $g(P)$.

The model is related to field observations gathered in the Bay of Bengal. On the basis of the data collected, the analysis and the simulations of the model, the authors conclude that toxin producing phytoplankton could be a relevant factor not only in the termination of the planktonic blooms, but also are able to self-regulate. The pressure exerted on the zooplankton forces a reduction of its grazing pressure, hindering its feeding ability. Toxic producing phytoplankton in this way could become a sort of biological control.

The model

$$\begin{cases} \dot{P} = rP\left(1 - \dfrac{P}{K}\right) - \alpha PZ \\ \dot{Z} = \beta PZ - cZ - \dfrac{\theta P}{\gamma + P} Z \end{cases} \tag{2}$$

and a version including a delay to account for a slow effect of the poison

$$\begin{cases} \dot{P} = rP\left(1 - \dfrac{P}{K}\right) - \alpha PZ \\ \dot{Z} = \beta PZ - cZ - \dfrac{\theta P(t-\tau)}{\gamma + P(t-\tau)} Z \end{cases} \tag{3}$$

are both considered in [26]. When the toxin release is istantaneous, blooms are not observed. Periodic blooms arise instead in the case of the delayed harmful effects of the toxin. Furthermore, the model is extended to encompass environmental stochastic fluctuations in the environment. There is a critical value for the delay, for which the coexistence equilibrium is stably achieved when the delay falls below this threshold, i.e. for slower fluctuations. Faster variations instead lead to coexistence equilibrium destabilization, from which persistent oscillations in the population values arise. The region of stability becomes larger for a less rapid artificial eutrophication, so that the latter favors termination of harmful planktonic blooms.

This concept is reelaborated in [11] using a model that exploits the Ornstein-Uhlenbeck process, [31], and extends it to a more realistic situation of three populations as follows

$$\begin{cases} \dot{P}_1 = rP_1\left(1 - \dfrac{P_1}{K}\right) - \alpha P_1 Z \\ \dot{P}_2 = sP_2\left(1 - \dfrac{P_2}{K}\right) - \dfrac{\theta P_2 Z}{\gamma + P_2} \\ \dot{Z} = \beta P_1 Z - \mu Z - \dfrac{\theta_1 P_2 Z}{\gamma + P_2}, \end{cases} \tag{4}$$

where Z denotes zooplankton, while P_1 and P_2 are the phytoplankton populations, of which only the latter is toxic. The grazing pressure of zooplankton is here assumed to be reduced by the presence of the poisonous phytoplankton P_2.

The toxic phytoplankton-free equilibrium is shown to be unstable, so that this population is persistent in the system and has a key role in reducing and possibly terminating blooms.

In [27] the study is extended considering a mathematical model made of two harmful phytoplankton populations and one zooplankton population. The system, written first in a general form, is therefore

$$\begin{cases} \dot{P}_1 = r_1 P_1 \left(1 - \dfrac{P_1}{K}\right) - \alpha P_1 P_2 - m P_1 Z \\ \dot{P}_2 = r_2 P_2 \left(1 - \dfrac{P_2}{L}\right) - \beta P_1 P_2 - n P_2 Z \\ \dot{Z} = (m_1 P_1 + n_1 P_2) Z - \mu Z - \theta_1 f(P_1) Z - \theta_2 g(P_2) Z \,. \end{cases} \tag{5}$$

Here P_1 and P_2 are the toxic phytoplankton populations, competing with each other, while Z as usual denotes the zooplankton. A number of properties of this system are derived, like boundedness of the trajectories, a characterization of the equilibria and conditions ensuring the persistence of the ecosystem. Then a specific formulation consists in replacing the functions f and g in the equation of the zooplankters by Holling type II response functions,

$$f(P_1) = \frac{P_1}{\gamma_1 + P_1}, \quad g(P_2) = \frac{P_2}{\gamma_1 + P_2}.$$

The analysis and the simulations together with a comparison with former research show that at equilibrium the population values of the three species appearing in the model become smaller, because two toxin releasing phytoplankton populations are present. Thus harmful phytoplankton helps in reducing the planktonic blooms levels. These results have been verified by the experimental activities performed on site in the eastern part of the Bay of Bengal.

The model considered in [25] replaces one of the toxic phytoplankton populations of (5), P_1, by a harmless phytoplankton. The system reads

$$\begin{cases} \dot{P}_1 = P_1 \left[r_1 \left(1 - \dfrac{P_1 + \alpha_1 P_2}{K}\right) - \dfrac{\omega_1 Z}{D_1 + P_1} \right] \\ \dot{P}_2 = P_2 \left[r_2 \left(1 - \dfrac{P_2 + \alpha_2 P_1}{K}\right) - \dfrac{\omega_2 Z}{D_2 + P_2} \right] \\ \dot{Z} = Z \left[\dfrac{\xi_1 P_1}{D_1 + P_1} - \dfrac{\xi_2 P_2}{D_2 + P_2} - c \right] \,. \end{cases} \tag{6}$$

It tries to address the question of “the paradox of the plankton”, raised in [19]. The issue argues on the possibility of coexistence of a large number of phytoplankton species on a seemingly limited variety of resources. The novel answer proposed here consists in the role exerted by toxin releasing phytoplankton in the whole ecosystem considered in the model. Toxin allelopathy reduces the phytoplankton interspecific competition. On the other hand, it also inhibits the growth of the zooplankton population.

A more elaborated model is introduced in [23], where also the nutrients for phytoplankton survival are taken into account, represented by the variable N in the following system

$$\begin{cases} \dot{N} = D\left(N^0 - N\right) - \alpha_1 PN + \mu_3 P + \mu_4 Z \\ \dot{P} = \alpha_2 PN - \gamma_1 PZ - (\mu_1 + D_1)P \\ \dot{Z} = \left(\gamma_2 - \dfrac{\theta}{\gamma + P}\right) PZ - (\mu_2 + D_2)Z\,. \end{cases} \tag{7}$$

The ecosystem persists at coexistence equilibrium when the maximal zooplankton feeding rate exceeds a certain value. The stability of the steady state is lost below this threshold, giving rise to a Hopf bifurcation leading to periodic blooms. The latter are related to very high nutrient concentrations.

Three models are introduced and discussed in [8], at first only considering the toxin-releasing phytoplankton and nutrient dynamics. This basic model had been already studied, [18], but it is extended to consider seasonal variations by the introduction of a Heaviside function $\beta(t)$. The first model is

$$\begin{cases} \dot{N} = a - b\beta(t)NP - eN \\ \dot{P} = c\beta(t)NP - dP\,. \end{cases} \tag{8}$$

A modification of the latter accounting for the fact that toxin release would be very low for a low phytoplankton population, contains instead the Holling type III response function, in place of linear mortality for the phytoplankton,

$$\begin{cases} \dot{N} = a - bNP - eN \\ \dot{P} = cNP - dP - \dfrac{\theta P^2}{\mu^2 + P^2}\,. \end{cases} \tag{9}$$

A further step consists in replacing the function β by a Holling type II term, as follows

$$\begin{cases} \dfrac{dN}{dt} = a - \dfrac{bNP}{\gamma + N} - eN, \\ \dfrac{dP}{dt} = \dfrac{cNP}{\gamma + N} - dP - \dfrac{\theta P^2}{\mu^2 + P^2}. \end{cases} \tag{10}$$

and the next model of [8] includes nutrient recycling

$$\begin{cases} \dfrac{dN}{dt} = a - bNP - eN + kP, \\ \dfrac{dP}{dt} = cNP - dP - \dfrac{\theta P^2}{\mu^2 + P^2}, \end{cases} \tag{11}$$

to obtain finally the most general model

$$\begin{cases} \dfrac{dN}{dt} = a - b\beta(t)NP - eN \\ \dfrac{dP}{dt} = c\beta(t)NP - dP - \dfrac{\theta(t) P^2}{\mu^2 + P^2}. \end{cases} \tag{12}$$

The latter enhances the possibility of recurring blooms, which attain chaotic behavior in certain circumstances. Higher concentrations of toxic chemicals could constitute a possible way of controlling the situation. A further variation of these concepts has also subsequently been explored and elaborated in [9]. The functional forms for modeling the toxin release seem to scantly influence the ultimate system's behavior. Logistic growth of phytoplankton is combined with a Holling type II grazing term. In addition to natural mortality, zooplankton experiences the effects of poison released by harmful phytoplankton. This is modeled via several possible functions.

The possibility that zooplankton reacts to the release of toxins by phytoplankton is first considered in [3]. This is modelled via a Monod-Haldane response function,

$$\begin{cases} \dot{P} = r_P P(1-P) - aPT - cPZ \\ \dot{T} = r_T T\left(1 - \dfrac{T}{H}\right) - bPT - \dfrac{TZ}{1+T^2} \\ \dot{Z} = ePZ - \dfrac{TZ}{1+T^2} - mZ\,. \end{cases} \tag{13}$$

The results indicate that this formulation prevents the zooplankton population being driven to extinction by the action of the toxin-releasing phytoplankton.

The insurgence of harmful red tides under appropriate conditions is obtained via simulations.

Also [28] contains a similar formulation in which the grazing is reduced in the same way as above, but on both phytoplankton populations.

$$\begin{cases} \dot{P} = r_P P \left(1 - \dfrac{P}{H_P}\right) - aPT - \dfrac{PZ}{1+P^2} \\ \dot{T} = r_T T \left(1 - \dfrac{T}{H_T}\right) - bPT - g\dfrac{TZ}{1+T^2} \\ \dot{Z} = e\dfrac{PZ}{1+P^2} - \dfrac{TZ}{1+T^2} - mZ\,. \end{cases} \tag{14}$$

In general, the analysis of the equilibria, which are the same as in the model (13), in this case leads to more stringent feasibility and stability conditions.

A different idea for the poison-releasing mechanism has been introduced in [12]. The model is much simpler, focusing just on the toxic phytoplankton P – zooplankton Z interaction,

$$\begin{cases} \dot{P} = rP - bP^2 - \dfrac{cfZP}{a+\gamma P} \\ \dot{Z} = \dfrac{efZP}{a+\gamma P} - \mu Z - e\rho P^{\frac{2}{3}} Z\,. \end{cases} \tag{15}$$

The assumption is that phytoplankton gathers to form lumps and the subsequent release of toxins upon attack by zooplankton occurs via the surface of these agglomerates. This very idea is at the heart of the models that we will introduce in the next Sections, we will indeed find the same nonlinear term that is present here in the second equation. The exponent $\frac{2}{3}$ is related to the surface area of the sphere, i.e. of an approximation of the lump. In fact, if the population P occupies a certain volume, more or less spherical, its radius is given by the cubic root of the volume, i.e. of the population size, and therefore the area of the spherical surface will be proportional to the square of the latter. Similar models have been recently considered in different ecological frameworks, [1,2,5,32,33]. The analysis shows that the gathering in patches by the toxin-producing phytoplankton somewhat inhibits the grazers. The analysis stresses the fact that the fraction of aggregated phytoplankton helps in a relevant way both the forming of recurrent blooms as well as the system to achieve a stable coexistence equilibrium. Thus patches could explain the phenomenon of monospecies blooms, present here but which is not observed in [10].

The basic idea is used once again in [13]. The model in this case is

$$\begin{cases} \dot{P} = rP - bP^2 - c(1-k)ZP \\ \dot{Z} = e(1-k)ZP - \mu Z - e\rho P^{\frac{2}{3}} Z \,. \end{cases} \tag{16}$$

Here it is observed that the poisonous phytoplankton gathered in patches reduces the zooplankton's grazing.

Before concluding this quick overlook of parts of the field, we mention also the paper [29], extending the classical Beretta-Kuang model [6]. Although not dealing expressly with plankton, these papers focus also on the aquatic environment, but this time viruses are considered in the model as well as bacteria. The system introduced in [29] considers also the dynamics of the viruses confined within and infecting the bacteria.

Finally, let us remark that in this Chapter we consider only the dynamical systems with no consideration of possible spatial effects, that have however been recently taken into account in [33] for plankton models with lumping features related to the ones discussed above. It is well known that patterns arise when space is introduced, and we just limit ourselves to refer the reader to the fairly recent book [22] for an account of these features, that we have here completely omitted for lack of space.

3. Underlying Assumptions

From now on, let Z denote the zooplankton, let P be the harmless phytoplankton, and T the toxic phytoplankton. We assume that Z feeds upon both phytoplankton populations, which are both edible, but the latter can react to the predators by releasing toxins and is therefore harmful to the zooplankton.

In line with the discussion we had in the Introduction, we formulate now our basic assumption, for which no experimental evidence is yet available. We specifically assume that the toxic phytoplankton agglomerates to constitute three-dimensional patches. Further, the release of the toxins by the toxic phytoplankton occurs through the surface of these patches. Since the latter could have any shape, but in any case the surface area is a measure of a two-dimensional quantity while the size of the patch is a three-dimensional one, the amount of toxin released would be proportional to the $\frac{2}{3}$ power of the population size in each patch. To be more specific, recalling what done in [2], to which we refer the reader for further details, assume that only a fraction $0 < k < 1$ of phytoplankton aggregates to form patches, and that there are N such patches. In each patch we then find $\frac{1}{N}kT$ phytoplanktons. The rate at which toxins are released depends then on the quantity

$$\left(\frac{1}{N}kT\right)^{\frac{2}{3}} = \rho T^{\frac{2}{3}}, \quad \rho \equiv \left(\frac{k}{N}\right)^{\frac{2}{3}}. \tag{17}$$

We have introduced the parameter ρ which in a sense is a measure of the toxic level. Through possibly the multiplication by another factor of geometric nature, which we assume for simplicity here incorporated into it, ρ can take care also of possible patch deformations from the spherical shape. A schematic illustration of the aquatic ecosystem is shown in Figure 1.

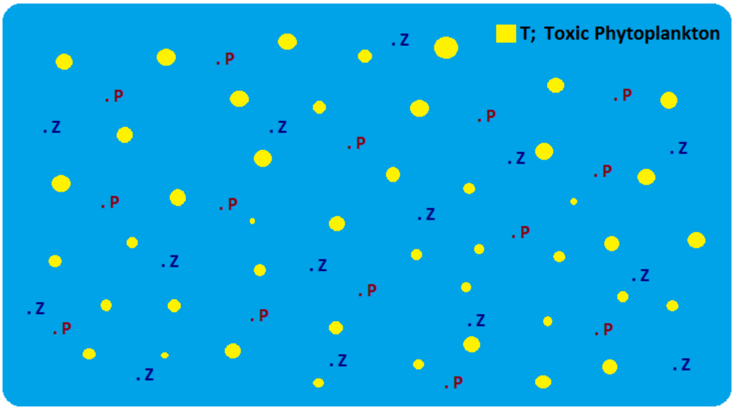

Figure 1. A sketch of the marine environment, where the yellow lumps denote toxic phytoplankton, the red dots the harmless phytoplankton and the black dots the zooplankton.

4. The First Model: Independent Phytoplankton Populations

In the first model, we assume that the two phytoplankton populations P and T grow independently from each other. Assuming from now on that all parameters are nonnegative, we have

$$
\begin{aligned}
\dot{P} &= r_P P\left(1-\frac{P}{K}\right) - a\frac{PZ}{b+P}\\
\dot{T} &= r_T T\left(1-\frac{T}{H}\right) - c\frac{TZ}{g+T}\\
\dot{Z} &= ae\frac{PZ}{b+P} + ce\frac{TZ}{g+T} - mZ - \rho T^{\frac{2}{3}}Z.
\end{aligned}
\tag{18}
$$

Here the first two equations show logistic growth for both the harmless and the toxic phytoplankton populations. We assume that the environment's carrying capacity is possibly different for the two populations and it is respectively denoted by K and H. The parameters r_P and r_T represent their respective net growth rates. The last term in each equation models the uptake mechanism due to zooplankton grazing. We use a Holling-type II function, to incorporate a more realistic zooplankton feeding satiation. The parameters a and c represent the maximum prey removal rates, b and g are the half saturation constants.

The last equation describes the time evolution of the zooplankton, which dies naturally at rate m and reproduces in a direct proportion to the prey uptake. However not all the biomass eaten is converted into new individuals, but only a fraction $0 < e < 1$, a parameter which is generally known as conversion factor. The last term in the zooplankton equation incorporates instead the loss of biomass due to the effect of the toxins released by the harmful phytoplankton, recalling (17).

It is easily seen that the Jacobian of model (18) has a singularity when $T = 0$. To remove this difficulty, we introduce a new variable X, such that $T = X^3$. Note that upon differentiation we find $\dot{T} = 3X^2\dot{X}$. The model (18) can then be rewritten as follows

$$
\begin{aligned}
\dot{P} &= r_P P\left(1-\frac{P}{K}\right) - \frac{aPZ}{b+P}\\
\dot{X} &= \frac{r_T X}{3}\left(1-\frac{X^3}{H}\right) - \frac{cXZ}{3\,(g+X^3)}\\
\dot{Z} &= \frac{aePZ}{b+P} + \frac{ceX^3Z}{g+X^3} - mZ - \rho X^2 Z\,.
\end{aligned}
\tag{19}
$$

4.1. Boundedness

Define the total system population $S = P + T + Z$. On summing the equations of (18) we find

$$\begin{aligned} \frac{dS}{dt} &= r_P P\left(1-\frac{P}{K}\right) - \frac{a(1-e)PZ}{b+P} + r_T T\left(1-\frac{T}{H}\right) - \frac{c(1-e)TZ}{g+T} - mZ - \rho T^{\frac{2}{3}} Z \\ &\leq r_P P\left(1-\frac{P}{K}\right) + r_T T\left(1-\frac{T}{H}\right) - mZ. \end{aligned} \tag{20}$$

since $0 < e < 1$. Now for $\phi < m$, we have the further inequalities

$$\begin{aligned} \frac{dS}{dt} + \phi S &\leq P\left[r_P\left(1-\frac{P}{K}\right)+\phi\right] + T\left[r_T\left(1-\frac{T}{H}\right)+\phi\right] - (m-\phi)Z \\ &\leq K\frac{(r_P+\phi)^2}{4r_P} + H\frac{(r_T+\phi)^2}{4r_P} = M^*, \end{aligned}$$

where to get the last estimate we have taken the maxima of each parabola on the right. Thus

$$S(t) \leq \exp(-\phi t)S(0) + \frac{M^*}{\phi}\left[1-\exp(-\phi t)\right] \leq \max\left\{S(0), \frac{M^*}{\phi}\right\}.$$

Since the sum of the populations is bounded, each individual population is also bounded.

4.2. Equilibria

We find the points: $Q_0 = (0,0,0)$, $Q_1 = (K,0,0)$ and $Q_2 = \left(0, \sqrt[3]{H}, 0\right)$. Further, the point $Q_3 = (0, X_3, Z_3)$, with no harmless phytoplankton, can be shown to exist in the following way. From the second equation of (18), we find

$$Z = \frac{r_T}{c}\left(g + X^3\right)\left(1 - \frac{X^3}{H}\right) \tag{21}$$

while we write the third one as $k(X) = h_1(X) - h_2(X) = 0$, where explicitly

$$k(X) \equiv \frac{ceX^3}{g+X^3} - m - \rho X^2$$

and

$$h_1(X) = \frac{ceX^3}{g+X^3}, \quad h_2(X) = m + \rho X^2.$$

These are a concave rational function and a convex quadratic function of X. In particular, $h_1 \to ce$ as $X \to +\infty$, while $h_2 \to +\infty$ as $X \to +\infty$. To annihilate k means to have the two curves meeting at some points. We thus need to find the intersections of these curves. Clearly, since $h_1(0) = 0$ and $h_2(0) = m > 0$, two intersections exist if the function h_2 raises very slowly, so as to allow the function $h_1(X)$ to raise up from the origin and meet $h_2(X)$. Let us rewrite k as

$$k(X) = \frac{(ce-m)X^3 - gm - \rho g X^2 - \rho X^5}{g+X^3} \equiv \frac{\mathcal{A}(X)}{g+X^3}.$$

We thus need to find the zeros of the numerator $\mathcal{A}(X)$. The algebraic problem is not so simple, so we will try to find sufficient conditions for asserting that these intersections exist.

Note that the function $\mathcal{A}(X)$ is negative at the origin, $\mathcal{A}(0) < 0$, and it is also negative for large X. If we impose that its maximum value is positive, by continuity at least two intersections with the X axis must then exist.

Calculating its derivative we find

$$\mathcal{A}'(X) = X\left[3(ce-m)X - 2\rho g - 5\rho X^3\right] = X\left[\mathcal{L}(X) - \mathcal{R}(X)\right],$$

where we let

$$\mathcal{L}(X) = 3(ce-m)X\ , \quad \mathcal{R}(X) = 2\rho g + 5\rho X^3\ .$$

Once again, the abscissae of the intersections of $\mathcal{L}$ and $\mathcal{R}$ give the points at which $\mathcal{A}$ attains its maxima and minima. Now $\mathcal{R}$ is a cubic, positive and always increasing; instead $\mathcal{L}$ is a straight line, positive for $X > 0$ if and only if

$$ce > m. \tag{22}$$

For the two functions $\mathcal{L}$ and $\mathcal{R}$ to meet for $X > 0$, this last condition must then be satisfied. Further, $\mathcal{L}(0) = 0$ and $\mathcal{R}(0) = 2\rho g > 0$. Hence, since $\mathcal{R}$ is convex, these functions either never meet or have two intersections. Consider the point $\widetilde{X}$ at which the slopes of $\mathcal{L}$ and $\mathcal{R}$ coincide. Since

$$\mathcal{L}'(X) = 3(ce-m)\ , \quad \mathcal{R}'(X) = 15\rho X^2$$

the slope of $\mathcal{R}$ increases with X, so that if we impose that at $\widetilde{X}$ the function $\mathcal{R}$ lies below $\mathcal{L}$, by continuity for some abscissae $\widehat{X} > \widetilde{X} > X_*$ the two functions must meet. To find the points $\widetilde{X}$ where the slopes coincide, we determine the solutions of the equation $\mathcal{L}^{'} = \mathcal{R}^{'}$, and retain the positive abscissa:

$$X^* = \sqrt{\frac{ce-m}{5\rho}}. \tag{23}$$

For the intersections to exist, we must then impose

$$\mathcal{R}(X^*) < \mathcal{L}(X^*). \tag{24}$$

At the point $\widehat{X}$ thus we have $\mathcal{A}'(\widehat{X}) = 0$. We now show that this is a maximum for $\mathcal{A}$. Since $\mathcal{L}^{'} < \mathcal{R}^{'}$ for $X > \widetilde{X}$, at $\widehat{X}$ we have $\mathcal{L}^{'}(\widehat{X}) < \mathcal{R}^{'}(\widehat{X})$, as well as $\mathcal{L}(\widehat{X}) = \mathcal{R}(\widehat{X})$. Calculating the second derivative of $\mathcal{A}$ we find

$$\mathcal{A}^{''}(X) = [\mathcal{L}(X) - \mathcal{R}(X)] + X\left[\mathcal{L}'(X) - \mathcal{R}'(X)\right],$$

and evaluation at $\widehat{X}$ gives

$$\mathcal{A}''\left(\widehat{X}\right) = \left[\mathcal{L}\left(\widehat{X}\right) - \mathcal{R}\left(\widehat{X}\right)\right] + \widehat{X}\left[\mathcal{L}'\left(\widehat{X}\right) - \mathcal{R}'\left(\widehat{X}\right)\right] = \widehat{X}\left[\mathcal{L}'\left(\widehat{X}\right) - \mathcal{R}'\left(\widehat{X}\right)\right] < 0,$$

thereby showing that at $\widehat{X}$ the function $\mathcal{A}$ has indeed a maximum. Imposing then

$$\mathcal{A}(\widehat{X}) > 0 \tag{25}$$

and if (22) and (24) hold, there are two intersections of the functions h_1 and h_2 as needed, giving the equilibrium values X_3^- and X_3^+ of the toxic phytoplankton population at equilibrium. Note that when (22) is not satisfied, the function $\mathcal{R}$ lies always above the function $\mathcal{L}$ and therefore no feasible intersections are possible. The condition (25) is not however usable, since $\widehat{X}$ is not known. But (24) shows that $\mathcal{A}(\widetilde{X}) > 0$, so that, since at $\widehat{X}$ the function $\mathcal{A}$ attains a maximum and thus it is increasing in $[\widetilde{X}, \widehat{X}]$, (25) follows imposing

$$\mathcal{A}(X^*) > 0. \tag{26}$$

In summary, observing that (22) is a consequence of (24), i.e. of the first of the conditions here below, so that we can omit it, for feasibility of $Q_3 = (0, X_3, Z_3)$, we need the explicit conditions

$$\begin{aligned} &2\rho g + 5\rho X^{*3} < 3\,(ce-m)\,X^*\,, \\ &(ce-m)\,X^{*3} > gm + \rho g X^{*2} + \rho X^{*5}\,. \end{aligned} \tag{27}$$

To determine the point $Q_4 = (P_4, 0, Z_4)$, from the first equation of (18) solving for Z we have

$$Z = \frac{r_P}{a}(b+P)\left(1-\frac{P}{K}\right),$$

and substituting into the third one, we find

$$er_P P\left(1-\frac{P}{K}\right) - \frac{mr_P}{a}(b+P)\left(1-\frac{P}{K}\right) = 0,$$

from which the harmless phytoplankton population level is easily found, and from the above equation,

$$P_4 = \frac{bm}{ae-m}.$$

The equilibrium is determined,

$$Q_4 = \left(P_4, 0, \frac{r_P be}{ae-m}\left(1-\frac{P_4}{K}\right)\right).$$

It has the feasibility conditions

$$ae > m, \quad P_4 = \frac{bm}{ae-m} < K. \tag{28}$$

We also easily find the point $Q_5 = \left(K, \sqrt[3]{H}, 0\right)$.

The coexistence equilibrium is very hard to assess. We will only establish its existence, under suitable assumptions. From the first two equations of (18) we find

$$Z = \frac{r_T}{c}\left(g+X^3\right)\left(1-\frac{X^3}{H}\right) = \frac{r_P}{a}(b+P)\left(1-\frac{P}{K}\right),$$

which can be regarded as the quadratic equation $AP^2+BP+C=0$ in the variable P, with coefficients that are functions of X as follows

$$A = \frac{r_P}{aK} > 0, \quad B = \frac{r_P}{aK}(b-K), \quad C = \frac{r_T}{c}\left(g+X^3\right)\left(1-\frac{X^3}{H}\right) - \frac{r_P b}{a}.$$

By Descarte's rule, of interest are the cases with either two positive roots, two variations of sign, or one positive root, one sign variation. We examine only the simplest situation that ensures uniqueness, finding sufficient conditions for the latter case to hold. In view of the fact that $A > 0$, we just need to require $C < 0$ to have a unique positive root.

Substituting into the third equation of (18), we have $\Psi(X)+\Phi(X)=\Theta(X)$ where

$$\Psi(T)=\frac{aeP_{\pm}(X)}{b+P_{\pm}(X)}, \quad \Phi(X)=\frac{ceX^3}{g+X^3}, \quad \Theta(X)=m+\rho X^2 .$$

For $X\to+\infty$: $\Psi+\Phi$ is bounded for X large, while $\Theta\to+\infty$. To have an intersection, it is then enough to require that at the origin these functions satisfy $\Psi(0)+\Phi(0)>\Theta(0)$ which implies

$$(ae-m)P_{\pm}(0)>mb, \tag{29}$$

so that the functions Ψ and Φ interlace at some point, which gives the desired toxic phytoplankton population level of the coexistence equilibrium.

In the following Table we summarize the equilibria situation so far.

Point	Feasibility Conditions for model (18)
$Q_0=(0,0,0)$	–
$Q_1=(K,0,0)$	–
$Q_2=\left(0,\sqrt[3]{H},0\right)$	–
$Q_3=(0,X_3,Z_3)$	$2\rho g+5\rho X^{*3}<3(ce-m)X^*$, $(ce-m)X^{*3}>gm+\rho gX^{*2}+\rho X^{*5}$
$Q_4=(P_4,0,Z_4)$	$P_4\equiv\frac{bm}{ae-m}<K$, $ae>m$
$Q_5=\left(K,\sqrt[3]{H},0\right)$	–
$Q_6=(P_6,X_6,Z_6)$	$C<0$, $(ae-m)P_{\pm}(0)>mb$

4.3. Stability

The Jacobian of (18) at a generic point (P,X,Z) reads

$$\mathcal{J}=\begin{pmatrix} J_{11} & 0 & -\frac{aP}{b+P} \\ 0 & J_{22} & -\frac{cX}{3(g+X^3)} \\ \frac{aebZ}{(b+P)^2} & \frac{3cegZX^2}{(g+X^3)^2}-2\rho ZX & J_{33} \end{pmatrix}$$

with

$$J_{11}=r_P\left(1-\frac{2}{K}P\right)-\frac{abZ}{(b+P)^2},$$

$$J_{22}=\frac{r_T}{3}\left(1-\frac{4}{H}X^3\right)-cZ\frac{g-2X^3}{3(g+X^3)^2},$$

$$J_{33}=\frac{aeP}{b+P}+\frac{ceX^3}{g+X^3}-m-\rho X^2 .$$

Now, Q_0, is unstable in view of the eigenvalues r_P, $\frac{1}{3}r_T$, $-m$. Similarly Q_1 and Q_2 are unstable, since their respective eigenvalues are

$$\frac{1}{3}r_T, \quad -r_P, \quad \frac{aeK}{b+K}-ml; \qquad -r_T, \quad r_P, \quad \frac{ceH}{g+H}-m-\rho H^{\frac{2}{3}}.$$

At Q_3 the Jacobian factorizes to give explicitly one eigenvalue, $r_P-\frac{a}{b}Z_3$ and the quadratic characteristic equation

$$\lambda^2-A\lambda+B=0, \tag{30}$$

where

$$A=\frac{r_T}{3}\left(1-\frac{4}{H}X_3^3\right)-cZ_3\frac{g-2X_3^3}{3\left(g+X_3^3\right)^2}, \quad B=\frac{cX_3^2Z_3}{3\left(g+X_3^3\right)}\left[\frac{3cegX_3}{\left(g+X_3^3\right)^2}-2\rho\right]. \tag{31}$$

For stability, we need to require then $A<0$, $B>0$.

To study A, substituting the equilibrium value of Z_3 into the coefficient, we find

$$\left(1-\frac{4}{H}X_3^3\right)\left(g+X_3^3\right)+\left(2X_3^3-g\right)\left(1-\frac{X_3^3}{H}\right)<0\,,$$

from which letting $Y=X^3$, we have the inequality

$$Y\left(1-\frac{g}{H}\right)-\frac{2}{H}Y^2<0\,,$$

which finally gives a lower bound for $H>g$, while for $H<g$ the condition is $X_3>0$, which coincides with feasibility:

$$X_3>\max\left\{0,\sqrt[3]{\frac{H-g}{2}}\right\}. \tag{32}$$

The stability condition further requires positivity of the coefficient B. It simplifies to give

$$\frac{3cegX_3}{\left(g+X_3^3\right)^2}>2\rho. \tag{33}$$

Finally, the first eigenvalue must be negative, i.e.

$$r_P<\frac{a}{b}\frac{r_T}{c}\left(g+X_3^3\right)\left(1-\frac{X_3^3}{H}\right). \tag{34}$$

At Q_4 again the Jacobian factorizes, to give one eigenvalue as

$$\lambda_1 = \frac{1}{3}\left(r_T - \frac{c}{g}Z_4\right) < 0\,, \tag{35}$$

which gives the first stability condition

$$Z_4 > \frac{r_T g}{c}. \tag{36}$$

The remaining quadratic, (30), has the coefficients

$$A = r_P\left(1 - \frac{2}{K}P_4\right) - \frac{abZ_4}{(b+P_4)^2}\,, \quad B = \frac{a^2 beP_4Z_4}{(b+P_4)^3} > 0\,, \tag{37}$$

We thus need to require $A < 0$, to have two negative roots. This amounts to

$$K\,(ae - m) < b\,(ae + m)\ . \tag{38}$$

Finally, we study Q_5. The eigenvalues are $-r_P$, $-r_T$ and then it is sufficient to impose the last one to be negative to achieve stability, namely

$$\frac{aeK}{b+K} + \frac{ceH}{g+H} < m + \rho H^{\frac{2}{3}}. \tag{39}$$

In summary we have

Point	Stability Conditions for model (18)
$Q_0 = (0,0,0)$	unstable
$Q_1 = (K,0,0)$	unstable
$Q_2 = \left(0,\sqrt[3]{H},0\right)$	unstable
$Q_3 = (0,X_3,Z_3)$	$\frac{3cegX_3}{\left(g+X_3^3\right)^2} > 2\rho$, $r_P < \frac{a}{b}\frac{r_T}{c}\left(g+X_3^3\right)\left(1-\frac{X_3^3}{H}\right)$, $X_3 > \max\left\{0, \sqrt[3]{\frac{H-g}{2}}\right\}$
$Q_4 = (P_4,0,Z_4)$	$Z_4 > \frac{r_T g}{c}$, $K\,(ae-m) < b\,(ae+m)$
$Q_5 = \left(K,\sqrt[3]{H},0\right)$	$\frac{aeK}{b+K} + \frac{ceH}{g+H} < m + \rho H^{\frac{2}{3}}$

4.4. Simulations

For the parameter values $r_P = 2$, $r_T = 3$, $K = 180$, $H = 100$, $a = 3$, $c = 1.5$, $g = 1$, $e = 1$, $m = 2$ and $\rho = 3$ we provide two different results. We find persistent oscillations for $b = 36$ around Q_4, see Figure 2. For $b = 42$ instead the equilibrium Q_4 is stable, Figure 3.

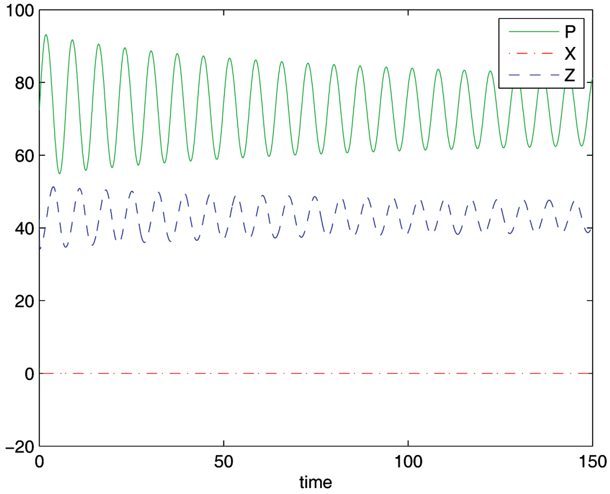

Figure 2. Time series solutions of model (18) for the parameter values $r_P = 2$, $r_T = 3$, $K = 180$, $H = 100$, $a = 3$, $c = 1.5$, $g = 1$, $e = 1$, $m = 2$, $\rho = 3$ and $b = 36$. We find persistent oscillations.

For the parameter values $r_P = 2$, $r_T = 4$, $K = 60$, $H = 250$, $a = 3$, $b = 1$, $c = 1$, $g = 4$, $e = 0.5$, $m = 1$ and $\rho = 1$ the equilibrium $Q_5\,(60; 6.29; 0)$ is stable, Fig. 4.

The coexistence equilibrium is stable for the parameters $r_P = 0.5$, $r_T = 1$, $K = 180$, $H = 100$, $a = 100$, $b = 500$, $c = 1.5$, $g = 1$, $e = 1$, $\rho = 0.1$ and $m = 15$, Fig. 5.

For $m = 1$ instead we find limit cycles, Fig. 6, Fig. 7.

4.5. Bifurcations and Their Structure

From the stability analysis, clearly Hopf bifurcations could arise only at the equilibria Q_3 and Q_4.

For Q_3, from (31), imposing $A = 0$ upon substitution of the explicit value of Z_3, we find

$$\frac{r_T}{3}\left(1-\frac{4}{H}X_3^3\right)-\frac{cg-2cX_3^3}{3\left(g+X_3^3\right)}\frac{r_T}{c}\left(g+X_3^3\right)\left(1-\frac{X_3^3}{H}\right)=X_3^3\left(1-\frac{g}{H}-\frac{2}{H}X_3^3\right)=0.$$

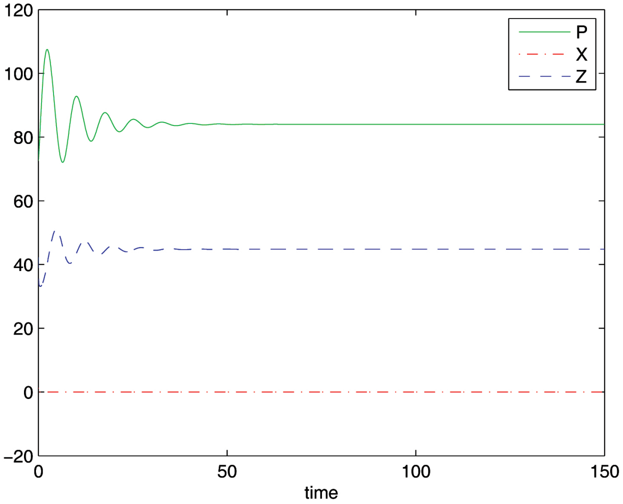

Figure 3. Time series solutions of model (18) for the parameter values as in Figure 2, but for $b = 42$. Here the toxic phytoplankton-free equilibrium is achieved.

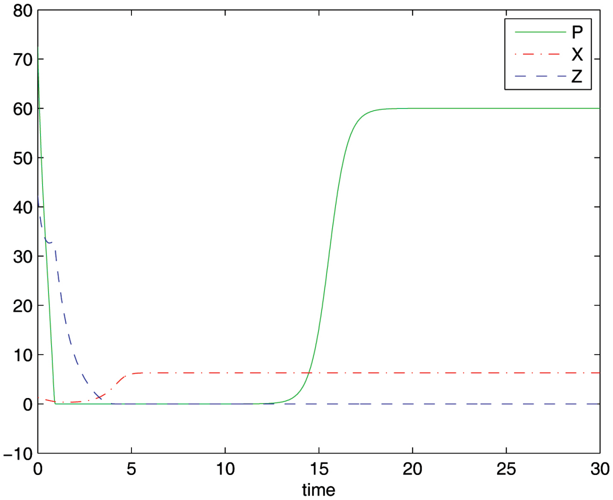

Figure 4. Equilibrium Q_5 is stably achieved for the parameter values $r_P = 2$, $r_T = 4$, $K = 60$, $H = 250$, $a = 3$, $b = 1$, $c = 1$, $g = 4$, $e = 0.5$, $m = 1$ and $\rho = 1$.

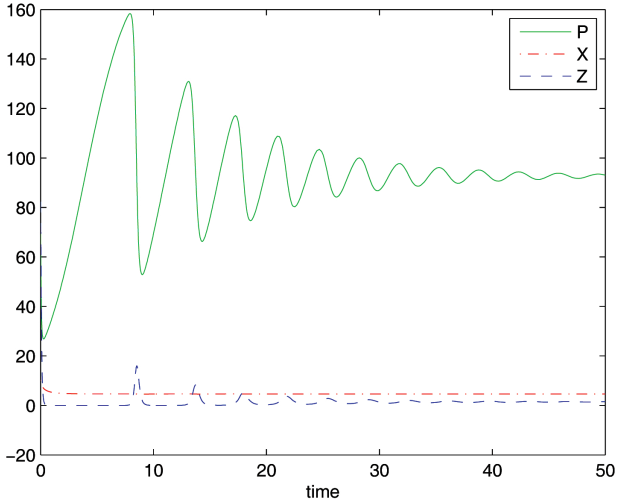

Figure 5. Coexistence equilibrium, attained for the parameter values $r_P = 0.5$, $r_T = 1$, $K = 180$, $H = 100$, $a = 100$, $b = 500$, $c = 1.5$, $g = 1$, $e = 1$, $\rho = 0.1$ and $m = 15$.

This condition holds when the carrying capacity H crosses the threshold

$$H^{\dagger} = g + 2X_3^3. \tag{40}$$

In case of Q_4, from (37) using the same technique we find that a Hopf bifurcation occurs when the corresponding carrying capacity crosses the threshold level

$$K^{\dagger} = \frac{b\,(ae+m)}{ae-m}\,. \tag{41}$$

Thus at Q_3 and Q_4 we have found Hopf bifurcations analytically. In the previous Subsection, we have numerically verified the occurrence for Q_4.

At $m = 18$ we have found numerically a transcritical bifurcation between Q_6 and Q_5.

Using Matcont, we further investigate the bifurcation structure as follows. For the choice of parameter values $r_P = .5$, $r_X = 1$, $K = 180$, $H = 100$, $a = 100$, $b = 500$, $c = 1.5$, $g = 1$ $e = 1$ $\rho = .1$ and $m = 4$ we find two interior equilibrium points $E_{1*}(16.019, 1.379, 2.350)$ and $E_{2*}(24.216, 4.587, 2.268)$. Both interior equilibrium points undergo a Hopf bifurcation at different thresholds of the pa-

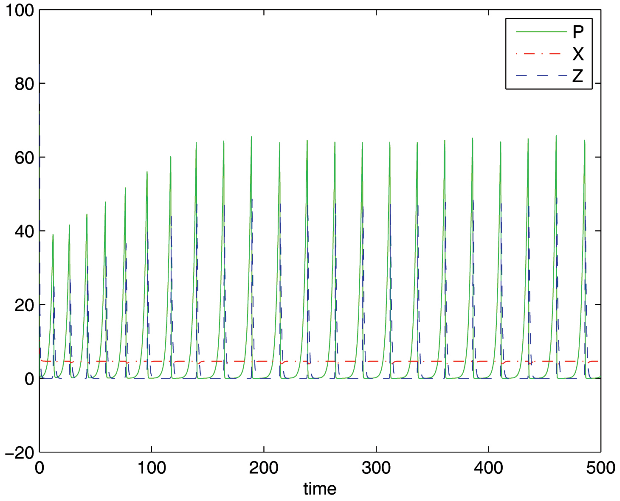

Figure 6. Limit cycles arise around the coexistence equilibrium for the same parameter values as in Figure 5, but for $m = 1$.

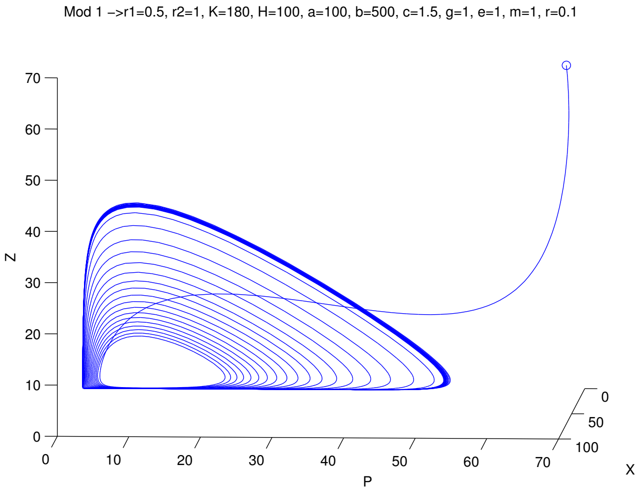
Mod 1 −>r1=0.5, r2=1, K=180, H=100, a=100, b=500, c=1.5, g=1, e=1, m=1, r=0.1

Figure 7. Phase space representation of Figure 6.

rameter m. E_{1*} emerges from a local bifurcation at the axial equilibrium point $(0, 1.42, 2.5)$ for $m = 0.91$. This bifurcation point is shown in Fig. 8.

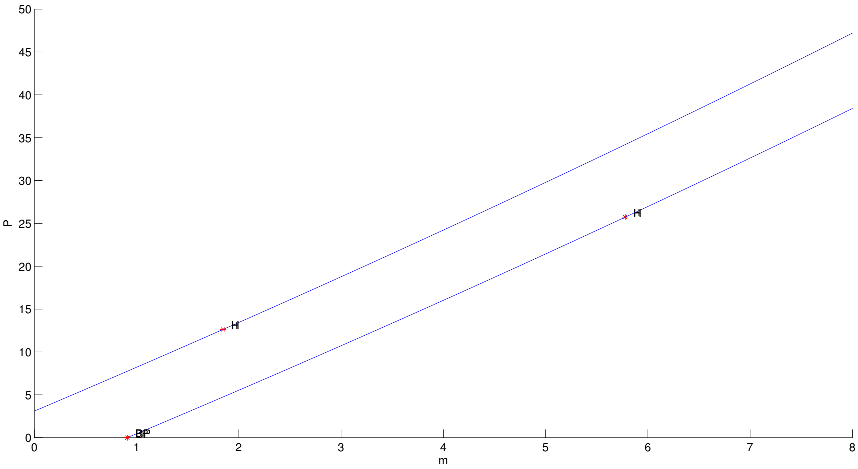

Figure 8. Using Matcont, the nontoxic phytoplankton P-component of the equilibrium points are plotted against m to show the bifurcations.

To identify the Hopf-bifurcation threshold we can continue the two equilibria with respect to the parameter m. The resulting plot of the P-component of two interior equilibrium points is presented in Fig. 8. If we look at the bifurcation diagram, we find that E_{1*} undergoes a subcritical Hopf-bifurcation at $m = 5.787$ while E_{2*} undergoes a supercritical Hopf-bifurcation at $m = 1.784$. As a result the Hopf-bifurcating limit cycle generated through Hopf-bifurcation is stable for $m < 1.784$. In such case E_{1*} becomes an unstable focus surrounded by a stable limit cycle. On the other hand, E_{2*} is stable for $m > 5.787$ and is surrounded by an unstable limit cycle. In Fig. 9 and Fig. 10 we have shown the continuation of Hopf-bifurcating limit cycles as function of m. The width of the limit cycles for non-toxic phytoplankton species is plotted against m. In Fig. 10 we can observe that the unstable limit cycle undergoes a saddle-node bifurcation of limit cycles at $m = 5.859$ where a stable and an unstable limit cycle collide with each other. In the same figure, we have shown the existence of two limit cycles for a range of values of m where the unstable limit cycle is surrounded by a stable limit cycle.

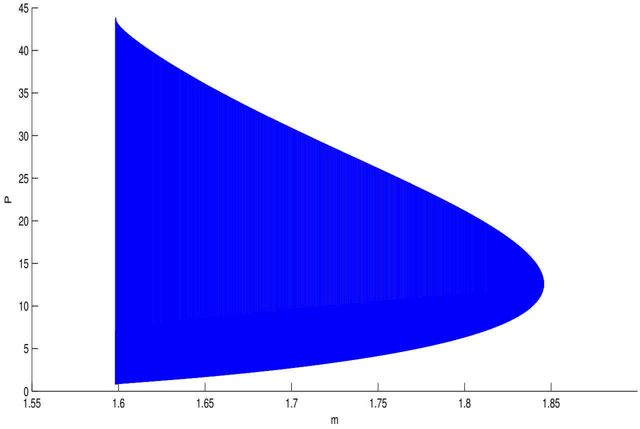

Figure 9. We find stable limit cycles for a range of values of m. Here the width of the limit cycle for the nontoxic phytoplankton P-component is plotted against m.

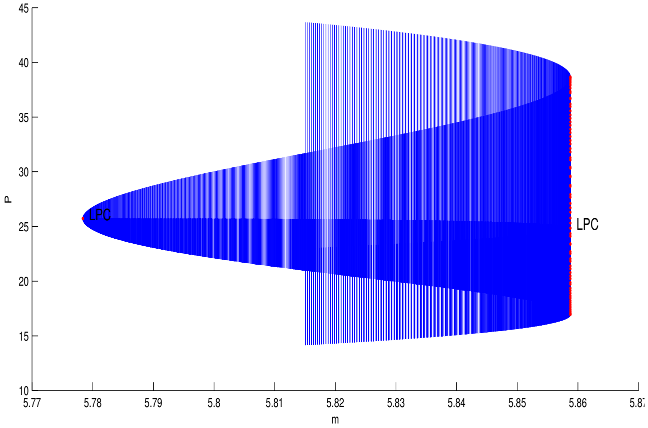

Figure 10. Subcritical Hopf bifurcation take place for $m = 5.7782$ and stable and unstable limit cycle collide with each other at $m = 5.859$. We find two limit cycles for a range of values of m.

5. The Second Model: Competing Phytoplankton Populations

We assume here once again that the zooplankton feeds on both phytoplankton populations and is harmed only when the toxic phytoplankton releases the poison. We further impose the specific assumption of this model, namely that in this case both phytoplankton populations have the same carrying capacity and both feel the population pressure of the other one, i.e. we have intraspecific competition. The new models is

$$\begin{aligned}\dot{P} &= r_P P\left(1-\frac{P+T}{K}\right)-a\frac{PZ}{b+P}\\ \dot{T} &= r_T T\left(1-\frac{P+T}{K}\right)-c\frac{TZ}{g+T}\\ \dot{Z} &= ae\frac{PZ}{b+P}+ce\frac{TZ}{g+T}-mZ-\rho T^{\frac{2}{3}}Z.\end{aligned} \tag{42}$$

Once again, we change the variable $T = X^3$ to obtain

$$\begin{aligned}\dot{P} &= r_P P\left(1-\frac{P+X^3}{K}\right)-\frac{aPZ}{b+P}\\ \dot{X} &= \frac{r_T X}{3}\left(1-\frac{P+X^3}{K}\right)-\frac{cXZ}{3\,(g+X^3)}\\ \dot{Z} &= \frac{aePZ}{b+P}+\frac{ceX^3Z}{g+X^3}-mZ-\rho X^2 Z\,.\end{aligned} \tag{43}$$

The parameters retain the meaning that they have in the system (18).

5.1. Boundedness

Again as for the first model we define the total population $S = P+T+Z$. Sum the equations of (42) and use a slight modification of the argument of (20), obtaining for $r = \max\{r_P, r_T\}$

$$\begin{aligned}\frac{dS}{dt} &= r_P P\left(1-\frac{P+T}{K}\right)-\frac{a(1-e)PZ}{b+P}+r_T T\left(1-\frac{P+T}{K}\right)-\frac{c(1-e)TZ}{g+T}\\ &\quad -mZ-\rho T^{\frac{2}{3}}Z \qquad (44)\\ &\le r(P+T)\left(1-\frac{P+T}{K}\right)-mZ\end{aligned}$$

in view of $0 < e < 1$. Introduce again $\phi < m$ to get, taking the maxima of the parabola,

$$\frac{dS}{dt} + \phi S \leq (P+T)\left[r\left(1 - \frac{P+T}{K}\right) + \phi\right] - (m-\phi)Z$$
$$\leq K\frac{(r+\phi)^2}{4r} = M_*.$$

Thus

$$S(t) \leq \exp(-\phi t)S(0) + \frac{M_*}{\phi}\left[1 - \exp(-\phi t)\right] \leq \max\left\{S(0), \frac{M_*}{\phi}\right\}.$$

This establishes boundedness of each population in the ecosystem.

5.2. Equilibria

Easily, we find the points that are always feasible, and which coincide with those of system (18): $\widehat{Q}_0 = (0,0,0)$, $\widehat{Q}_1 = (K,0,0)$ and $\widehat{Q}_2 = \left(0, \sqrt[3]{K}, 0\right)$. Also the point $\widehat{Q}_3$ is the same as for (18), so that it is feasible only when conditions (27) hold. Once again, $\widehat{Q}_4$ is the same as for model (18), thus the feasibility conditions are once again (28).

For $\widehat{Q}_5$ in this case we find a line of equilibria, i.e. we lose uniqueness, as the equilibrium equations reduce to just

$$\frac{P + X^3}{K} = 1.$$

Thus for $\ell \in (0, K)$ we have

$$\widehat{Q}_5 = \left(\ell, \sqrt[3]{K-\ell}, 0\right). \tag{45}$$

For the coexistence equilibrium $\widehat{Q}_6$, we follow the steps of the previous Section. From the first two equations of (42), we solve for Z, getting

$$\frac{r_P}{a}(b+P) = \frac{r_T}{c}\left(g + X^3\right).$$

We can thus find the equilibrium value of the nontoxic phytoplankton population

$$\widehat{P}_6 = \frac{ar_T}{cr_P}\left(g + {X_6}^3\right) - b, \tag{46}$$

which in turn gives the first feasibility condition

$$\widehat{X}_6 > \sqrt[3]{\frac{bcr_P - agr_T}{ar_P}}. \tag{47}$$

Upon substitution of this value into the third equation, we have an equation that we write as $J(X) = H(X) + K(X)$, where

$$J(X) = 1 + \frac{cX^3}{a(g+X^3)}, \quad H(X) = \frac{cbr_P}{ar_T(g+X^3)}, \quad K(X) = \frac{1}{ae}\left(m + \rho X^2\right).$$

For $X \to +\infty$ we have $J(X) \to 1 + \frac{c}{a}$ while $H(X) + K(X) \to \infty$. To have a unique intersection of these curves, we require $H(0) + K(0) < J(0)$, namely

$$\frac{cbr_P}{agr_T} + \frac{m}{ae} < 1\,. \tag{48}$$

In summary

Point	Feasibility Conditions for model (42)
$\widehat{Q}_0 = Q_0 = (0,0,0)$	–
$\widehat{Q}_1 = Q_1 = (K,0,0)$	–
$\widehat{Q}_2 = Q_2 = \left(0,\sqrt[3]{K},0\right)$	–
$\widehat{Q}_3 = Q_3 = (0,X_3,Z_3)$	$2\rho g + 5\rho X^{*3} < 3(ce-m)X^*$, $(ce-m)X^{*3} > gm + \rho g X^{*2} + \rho X^{*5}$
$\widehat{Q}_4 = Q_4 = (P_4,0,Z_4)$	$P_4 \equiv \frac{bm}{ae-m} < K$, $ae > m$
$\widehat{Q}_5 = \left(\ell,\sqrt[3]{K-\ell},0\right)$	$\ell \in (0,K)$
$\widehat{Q}_6 = \left(\widehat{P}_6,\widehat{X}_6,\widehat{Z}_6\right)$	$\frac{cbr_P}{agr_T} + \frac{m}{ae} < 1$, $\widehat{X}_6 > \sqrt[3]{\frac{bcr_P - agr_T}{ar_P}}$

5.3. Stability

In this case the Jacobian is

$$\mathcal{J} = \begin{pmatrix} J_{11} & -\frac{3r_P}{K}PX^2 & -\frac{aP}{b+P} \\ -\frac{r_T}{3K}X & J_{22} & -\frac{cX}{3(g+X^3)} \\ \frac{aebZ}{(b+P)^2} & \frac{3cegX^2Z}{(g+X^3)^2} - 2\rho XZ & J_{33} \end{pmatrix}$$

with

$$J_{11}=r_P\left(1-\frac{2}{K}P\right)-\frac{r_P}{K}X^3-\frac{abZ}{(b+P)^2}\,,$$
$$J_{22}=\frac{r_T}{3}\left(1-\frac{P}{K}\right)-\frac{4r_T}{3K}X^3-cZ\frac{g-2X^3}{3\,(g+X^3)^2}\,,$$
$$J_{33}=\frac{aeP}{b+P}+\frac{ceX^3}{g+X^3}-m-\rho X^2\,.$$

The origin remains unstable, the points $\widehat{Q}_1$ and $\widehat{Q}_2$ are also in view of a zero eigenvalue. Respectively, their eigenvalues are

$$\begin{array}{lll}\lambda_1=-r_P\,, & \lambda_2=0\,, & \lambda_3=\frac{aeK}{b+K}-m<0\,;\\ \lambda_1=-r_T\,, & \lambda_2=0\,, & \lambda_3=\frac{ceK}{g+K}-m-\rho\sqrt[3]{K^2}<0\,.\end{array}$$

In fact, perturbing $\widehat{Q}_1$ by a small $\varepsilon>-K$, $\eta>0$, $\xi>0$, for which we have an initial condition near the equilibrium point, $\widehat{Q}_1^{(0)}\,(K+\varepsilon,\eta,\xi)$, we find

$$\begin{aligned}\frac{dP}{dt}&=r_P\,(K+\varepsilon)\left(1-\frac{K+\varepsilon+\eta^3}{K}\right)-a\frac{(K+\varepsilon)\,\xi}{b+K+\varepsilon}\\&=-\left[r_P\left(1+\frac{\varepsilon}{K}\right)\left(\varepsilon+\eta^3\right)+a\frac{\xi}{1+\frac{b}{K+\varepsilon}}\right].\end{aligned}$$

For stability we require this derivative to be negative, i.e. considering only first order terms, we get that the inequality is satisfied if we take

$$\varepsilon>-\min\left\{K,\frac{aK}{r_P(b+K)}\xi\right\}. \tag{49}$$

Further,

$$\frac{dX}{dt}=\frac{r_T}{3}\eta\left(1-\frac{K+\varepsilon+\eta^3}{K}\right)-\frac{c\eta\xi}{3\,(g+\eta^3)}=-\left[\frac{r_T\varepsilon\eta}{K}+\frac{r_T\eta^4}{K}+\frac{c\eta\xi}{g+\eta^3}\right]<0$$

which also clearly holds if ε is chosen so that

$$\varepsilon>-\left[\eta^3+\frac{Kc\xi}{r_T\,(g+\eta^3)}\right]. \tag{50}$$

For the last condition, we find

$$\frac{dZ}{dt}=\frac{ae\,(K+\varepsilon)\,\xi}{b+K+\varepsilon}-ce\frac{\eta^3\xi}{g+\eta^3}-m\xi-\rho\eta^2\xi=\frac{G_1(\varepsilon,\eta,\xi)}{(b+K+\varepsilon)(g+\eta^3)}<0,$$

if and only if $G_1<0$, where

$$\begin{aligned} G_1(\varepsilon,\eta,\xi) \quad &:= ae\,(K+\varepsilon)\,\xi(g+\eta^3)+ce\eta^3\xi(b+K+\varepsilon)\\ &\quad -\left(m\xi+\rho\eta^2\xi\right)(b+K+\varepsilon)(g+\eta^3). \end{aligned}$$

Considering the first order terms, this gives

$$aeKg\xi-(b+K)gm\xi<0,$$

from which Z decreases under the following condition

$$aeK<(b+K)m, \tag{51}$$

which corresponds to $\lambda_3<0$. However, clearly since the perturbations are arbitrary, we can always choose η and ξ so that neither (49) nor (50) hold. Hence the equilibrium $\widehat{Q}_1$ is unstable.

We proceed similarly for $\widehat{Q}_2$, using as initial condition $\widehat{Q}_2^{(0)}\left(\varepsilon,\sqrt[3]{K+\eta},\xi\right)$, with $\eta>-K$, $\varepsilon>0$, $\xi>0$. We find similar conditions for the first two differential equations. We have that the derivative of P is negative for

$$-r_p\varepsilon\left(\frac{\varepsilon+\eta}{K}\right)-\frac{a\varepsilon\xi}{b+\varepsilon}<0,$$

giving the restriction

$$\eta>-\varepsilon-\frac{aK\xi}{br_P}. \tag{52}$$

Also, the derivative of X is negative for

$$-\frac{1}{3}\sqrt[3]{K+\eta}\left[\frac{r_T}{K}(\eta+\varepsilon)+\frac{c\xi}{g+K+\eta}\right]<0,$$

leading to

$$\eta>-\varepsilon-\frac{cK\xi}{r_T(g+K)}. \tag{53}$$

The last one gives

$$\frac{dZ}{dt} = \frac{ae\varepsilon\xi}{b+\varepsilon} + \frac{ce\,(K+\eta)\,\xi}{g+K+\eta} - m\xi - \rho\sqrt[3]{(K+\eta)^2}\xi = \frac{G_2(\varepsilon,\eta,\xi)}{(b+\varepsilon)(g+K+\eta)}$$

where

$$\begin{aligned} G_2(\varepsilon,\eta,\xi) &= ae\varepsilon\xi(g+K+\eta) + ce\xi(K+\eta)(b+\varepsilon) \\ &\quad -\xi(m+\rho\sqrt[3]{(K+\eta)^2})(b+\varepsilon)(g+K+\eta). \end{aligned}$$

To have a negative derivative, it is then enough to impose $G_2 < 0$. Considering the first order terms, we are then led to

$$bce < (m+\rho\sqrt[3]{K^2})b(g+K), \tag{54}$$

which corresponds to $\lambda_3 < 0$. Again, given that ε and ξ are arbitrary, (52) and (53) in general are not satisfied, so that $\widehat{Q}_2$ is unstable.

For $\widehat{Q}_3$ we can find one eigenvalue explicitly, the same that is found for the first model (18), namely

$$\lambda_1 = r_P - \frac{r_P}{K}X_3^3 - \frac{a}{b}Z_3, \tag{55}$$

giving thus again the stability condition (34), and the quadratic equation (30) with the same B but where now the coefficient A becomes

$$A = \frac{r_T}{3}\left(1 - \frac{4}{K}X_3^3\right) - cZ_3\frac{g-2X_3^3}{3\left(g+X_3^3\right)^2},$$

in view of the fact that here $H = K$. We have stability if in addition to (34) also (33) holds and requiring $A < 0$, in place of (32) we find now

$$r_P < \frac{r_P}{K}X_3^3 + \frac{a}{b}Z_3. \tag{56}$$

At $\widehat{Q}_4$, the negativity of the first eigenvalue gives

$$Z_4 > \frac{gr_T}{c}\left(1 - \frac{P_4}{K}\right). \tag{57}$$

The remaining ones are the roots of the same quadratic (30) we had for (18) for the corresponding equilibrium Q_4, with the very same coefficients (37), so that to achieve stability together with (57) we find once again condition (38).

For $Q_5 = \left(\ell, \sqrt[3]{K-\ell}, 0\right)$ the first eigenvalue is negative for

$$\frac{ae\ell}{b+\ell} + \frac{ce\,(K-\ell)}{g+K-\ell} < m + \rho(K-\ell)^{\frac{2}{3}}. \tag{58}$$

The roots of the quadratic (30) with

$$A = -\left(\frac{r_P\ell}{K} + \frac{r_T\ell}{K} + r_T\right) < 0, \quad B = \frac{2r_Pr_T\ell^2}{K^2} > 0,$$

give the remaining eigenvalues, but the Routh-Hurwitz conditions show that they have always negative real part. Thus stability hinges just on (58).

In summary

Point	Stability Conditions for model (42)
$\widehat{Q}_0 = Q_0 = (0,0,0)$	unstable
$\widehat{Q}_1 = Q_1 = (K,0,0)$	unstable
$\widehat{Q}_2 = Q_2 = \left(0, \sqrt[3]{K}, 0\right)$	unstable
$\widehat{Q}_3 = Q_3 = (0, X_3, Z_3)$	$\frac{3cegX_3}{\left(g+X_3^3\right)^2} > 2\rho$, $r_P < \frac{a}{b}\frac{r_T}{c}\left(g+X_3^3\right)\left(1-\frac{X_3^3}{H}\right)$, $r_P < \frac{r_P}{K}X_3^3 + \frac{a}{b}Z_3$
$\widehat{Q}_4 = Q_4 = (P_4, 0, Z_4)$	$\frac{c}{gr_T}Z_4 + \frac{1}{K}P_4 > 1$, $K\,(ae-m) < b\,(ae+m)$
$\widehat{Q}_5 = (\ell, K-\ell, 0)$	$\frac{ae\ell}{K+\ell} + \frac{ce(K-\ell)}{g+K-\ell} < m + \rho(K-\ell)^{\frac{2}{3}}$

5.4. Bifurcations

In the context of model (42) no transcritical bifurcations arise.

At $\widehat{Q}_3$ only the first eigenvalue changes with respect to Q_3, so that a Hopf bifurcation arises exactly as it does for Q_3, namely for the carrying capacity crossing the critical value

$$K^{\dagger} = g + 2X_3^3, \tag{59}$$

i.e. replacing H by K in (40).

Similarly at $\widehat{Q}_4$ only the first eigenvalue differs from those of Q_4. The Hopf bifurcation is achieved when (41) holds.

6. Independently Growing and Competing Phytoplanktons

Here, the two phytoplanktons grow independently of each other, but do compete for common resources at respective rates h and k for the harmless and toxic populations. The parameters retain their meaning from the previous models (18) and (42).

$$\begin{aligned}\dot{P} &= r_P P\left(1-\frac{P}{K}\right)-kPT-a\frac{PZ}{b+P}\\ \dot{T} &= r_T T\left(1-\frac{T}{H}\right)-hPT-c\frac{TZ}{g+T}\\ \dot{Z} &= ae\frac{PZ}{b+P}+ce\frac{TZ}{g+T}-mZ-\rho T^{\frac{2}{3}}Z\,,\end{aligned} \tag{60}$$

The reformulation to avoid singularities leads to

$$\begin{aligned}\dot{P} &= r_P P\left(1-\frac{P}{K}\right)-kPX^3-\frac{aPZ}{b+P}\\ \dot{X} &= \frac{r_T X}{3}\left(1-\frac{X^3}{H}\right)-\frac{h}{3}PX-\frac{cXZ}{3\,(g+X^3)}\\ \dot{Z} &= \frac{aePZ}{b+P}+\frac{ceX^3Z}{g+X^3}-mZ-\rho X^2 Z\,.\end{aligned} \tag{61}$$

6.1. Boundedness

Let once again $S = P+T+Z$ and sum the equations of (60) to find this time

$$\begin{aligned}\frac{dS}{dt} &= r_P P\left(1-\frac{P}{K}\right)-kPT-\frac{a(1-e)PZ}{b+P}+r_T T\left(1-\frac{T}{H}\right)\\ &-hPT-\frac{c(1-e)TZ}{g+T}-mZ-\rho T^{\frac{2}{3}}Z \le r_P P\left(1-\frac{P}{K}\right)+r_T T\left(1-\frac{T}{H}\right)-mZ,\end{aligned} \tag{62}$$

so we find again the last estimate (20) of the first model, from which the remaining part of the proof is the same.

6.2. Equilibria

The points $\widetilde{Q}_0$, $\widetilde{Q}_1$, $\widetilde{Q}_2$, $\widetilde{Q}_3$ and $\widetilde{Q}_4$ are the same equilibria we found for model (19). Hence the feasibility conditions (27) and (28) for the latter two equilibria still hold.

For $\widetilde{Q}_5 = \left(\widetilde{P}_5, \widetilde{X}_5, 0\right)$, we can solve the first equation to get

$$P = \frac{K}{r_P}\left(r_P - kX^3\right)\,,$$

and substitution into the second one gives

$$\widetilde{X}_5 = \sqrt[3]{\frac{r_P H\left(r_T - Kh\right)}{r_T r_P - HKhk}}, \tag{63}$$

which in turn gives

$$\widetilde{P}_5 = \frac{r_T K\left(r_P - Hk\right)}{r_T r_P - HKhk}. \tag{64}$$

The feasibility conditions are one of the two alternative sets

$$\begin{aligned} &r_P - Hk > 0, \quad r_T - Kh > 0, \quad r_T r_P - HKhk > 0; \\ &r_P - Hk < 0, \quad r_T - Kh < 0, \quad r_T r_P - HKhk < 0. \end{aligned} \tag{65}$$

We finally provide sufficient conditions for the existence of the interior equilibrium $\widetilde{Q}_6$. Equating the first two equations of (61) we have

$$Z = \left(g + X^3\right)\left[\frac{r_T}{c}\left(1 - \frac{X^3}{H}\right) - \frac{h}{c}P\right] = \left(b + P\right)\left[\frac{r_P}{a}\left(1 - \frac{P}{K}\right) - \frac{k}{a}X^3\right],$$

which gives a quadratic equation in P, $AP^2 + BP + C = 0$ with

$$A = \frac{r_P}{aK} > 0, \quad B = -\frac{h}{c}\left(g + X^3\right) - \frac{r_P}{a}\left(1 - \frac{b}{K}\right) + \frac{k}{a}X^3,$$
$$C = \frac{r_T}{c}\left(1 - \frac{X^3}{H}\right)\left(g + X^3\right) + \frac{b}{a}\left(kX^3 - r_P\right).$$

If we apply Descartes' rule to have at least one positive root, we need to have $C < 0$ independently of the sign of B. The third equation of (61) is rewritten as $\Psi(X) + \Phi(X) = \Theta(X)$ with

$$\Psi(X) = \frac{aeP_{\pm}(X)}{b + P_{\pm}(X)}, \quad \Phi(X) = \frac{ceX^3}{g + X^3}, \quad \Theta(X) = m + \rho X^2.$$

As for (19), for $X \to +\infty$ the function $\Psi + \Phi$ is unbounded, while $\Theta \to +\infty$ for $X \to +\infty$. We obtain once again

$$P_{\pm}(0) > \frac{mb}{ae - m}, \tag{66}$$

showing the existence of $\widetilde{Q}_6$.

In summary

Point	Feasibility Conditions for model (60)
$\widetilde{Q}_0 = Q_0 = (0,0,0)$	–
$\widetilde{Q}_1 = Q_1 = (K,0,0)$	–
$\widetilde{Q}_2 = Q_2 = \left(0,\sqrt[3]{H},0\right)$	–
$\widetilde{Q}_3 = Q_3 = (0,X_3,Z_3)$	$2\rho g + 5\rho X^{*3} < 3\,(ce-m)X^*$, $(ce-m)X^{*3} > gm + \rho g X^{*2} + \rho X^{*5}$
$\widetilde{Q}_4 = Q_4 = (P_4,0,Z_4)$	$P_4 \equiv \frac{bm}{ae-m} < K$, $ae > m$
$\widetilde{Q}_5 = \left(\widetilde{P}_5,\widetilde{X}_5,0\right)$	$r_P - Hk > 0, \quad r_T - Kh > 0, \quad r_T r_P - HKhk > 0;$ or $r_P - Hk < 0, \quad r_T - Kh < 0, \quad r_T r_P - HKhk < 0$
$\widetilde{Q}_6 = \left(\widetilde{P}_6,\widetilde{X}_6,\widetilde{Z}_6\right)$	$P_{\pm}\,(0) > \frac{mb}{ae-m}$

6.3. Stability

The Jacobian in this case is

$$\mathcal{J} = \begin{pmatrix} J_{11} & -3kPX^2 & -\frac{aP}{b+P} \\ -\frac{h}{3}X & J_{22} & -\frac{cX}{3(g+X^3)} \\ \frac{aebZ}{(b+P)^2} & \frac{3cegZX^2}{(g+X^3)^2} - 2\rho ZX & J_{33} \end{pmatrix}$$

with

$$J_{11} = r_P\left(1 - \frac{2}{K}P\right) - kX^3 - \frac{abZ}{(b+P)^2}\,,$$

$$J_{22} = \frac{r_T}{3}\left(1 - \frac{4}{H}X^3\right) - \frac{h}{3}P - cZ\frac{g-2X^3}{3\,(g+X^3)^2}\,,$$

$$J_{33} = \frac{aeP}{b+P} + \frac{ceX^3}{g+X^3} - m - \rho X^2\,.$$

The origin, $\widetilde{Q}_0$, is unstable, in view of the eigenvalues r_P, $\frac{1}{3}r_T$, $-m$.

At $\widetilde{Q}_1$ we find $-r_P$ and the stability conditions stemming from the remaining eigenvalues

$$r_T < hK, \quad \frac{aeK}{b+K} < m. \tag{67}$$

A similar situation holds for $\widetilde{Q}_2$, in which case we find $-r_T$ and the conditions

$$r_P < kH, \quad \frac{ceH}{g+H} < m + \rho H^{\frac{2}{3}}. \tag{68}$$

For $\widetilde{Q}_3$ we require negativity of the first eigenvalue

$$r_P < k\widetilde{X}_3^3 + \frac{a}{b}\widetilde{Z}_3. \tag{69}$$

We then have the quadratic (30), already introduced in model (19), with the very same coefficients (31). We then impose $A < 0$ and $B > 0$ and find again conditions (32) and (33), which then give stability of $\widetilde{Q}_3$ together with (69).

For $\widetilde{Q}_4$ the condition on the first eigenvalue is

$$r_T < h\widetilde{P}_4 + \frac{c}{g}\widetilde{Z}_4. \tag{70}$$

The remaining quadratic characteristic equation is once again (30) where the coefficients have once more been dealt with earlier in model (19). They are indeed (37), giving for stability again condition (38) in addition to (70).

At $\widetilde{Q}_5$ the first eigenvalue produces the condition

$$\frac{ae\widetilde{P}_5}{b+\widetilde{P}_5} + \frac{ce\widetilde{X}_5^3}{g+\widetilde{X}_5^3} < m + \rho\widetilde{X}_5^2, \tag{71}$$

which bears some resemblance with (39) but is a bit more involved since $\widetilde{X}_5$ has a more complex representation than X_5. We have then once more the quadratic (30) with the coefficients

$$A = r_P\left(1 - \frac{2}{K}\widetilde{P}_5\right) - k\widetilde{X}_5^3 + \frac{r_T}{3}\left(1 - \frac{4}{H}\widetilde{X}_5^3\right) - \frac{h}{3}\widetilde{P}_5\,, \tag{72}$$

$$B = \left[r_P\left(1 - \frac{2}{K}\widetilde{P}_5\right) - k\widetilde{X}_5^3\right]\left[\frac{r_T}{3}\left(1 - \frac{4}{H}\widetilde{X}_5^3\right) - \frac{h}{3}\widetilde{P}_5\right] - kh\widetilde{P}_5\widetilde{X}_5^3\,.$$

Taking $B > 0$ and $A < 0$ ensures negativity of its roots. Now $A < 0$ can be restated as

$$\frac{3r_P + r_T}{3} - \widetilde{P}_5\left(\frac{2}{K}r_P + \frac{h}{3}\right) - \widetilde{X}_5^3\left(k + \frac{4r_T}{3H}\right) < 0\,,$$

so that by substituting the equilibrium coordinates and simplifying we obtain

$$r_P r_T hK + r_P r_T kH - r_P^2 r_T - r_P r_T^2 < 0\,,$$

from which

$$(r_T - hK) + (r_P - kH) > 0\,, \tag{73}$$

which holds if the first set of feasibility conditions (65) is satisfied. Otherwise, if the second set of (65) holds true, $\widetilde{Q}_5$ is unstable. The condition $B > 0$ becomes

$$r_T r_P \left(r_T r_P - hkKH\right)\left(r_T - hK\right)\left(r_P - kH\right) > 0$$

from which $r_T r_P > hkKH$, which is seen to be always satisfied using again the first set of feasibility conditions (65).

In summary

Point	Stability Conditions for model (60)
$\widetilde{Q}_0 = Q_0 = (0,0,0)$	unstable
$\widetilde{Q}_1 = Q_1 = (K,0,0)$	$r_T < hK,\ \frac{aeK}{b+K} < m$
$\widetilde{Q}_2 = Q_2 = \left(0,\sqrt[3]{H},0\right)$	$r_P < kH,\ \frac{ceH}{g+H} < m + \rho H^{\frac{2}{3}}$
$\widetilde{Q}_3 = Q_3 = (0,X_3,Z_3)$	$r_P < kX_3^3 + \frac{a}{b}Z_3,\ \frac{3cegX_3}{\left(g+X_3^3\right)^2} > 2\rho,\ X_3 > \max\left\{0, \sqrt[3]{\frac{H-g}{2}}\right\}$
$\widetilde{Q}_4 = Q_4 = (P_4,0,Z_4)$	$r_T < hP_4 + \frac{c}{g}Z_4,\ K\,(ae-m) < b\,(ae+m)$
$\widetilde{Q}_5 = \left(\widetilde{P}_5,\widetilde{X}_5,0\right)$	$\frac{ae\widetilde{P}_5}{b+\widetilde{P}_5} + \frac{ce\widetilde{X}_5^3}{g+\widetilde{X}_5^3} < m + \rho \widetilde{X}_5^2,$ $r_P > Hk,\ r_T > Kh,\ r_T r_P > HKhk$

6.4. Bifurcations

For the equilibria $\widetilde{Q}_3$ and $\widetilde{Q}_4$ since they are the same as for model (19), we find the same Hopf bifurcations, whose onset occurs when either (40) or (41) are satisfied.

For $\widetilde{Q}_5$ we need to annihilate the coefficient A given in (72), giving condition (73) replaced by an equality. But the latter then states that $\widetilde{Q}_5$ attains the border of the feasibility region, (65). Hence no Hopf bifurcations arise in this case.

We have a transcritical bifurcation between $\widetilde{Q}_6$ and $\widetilde{Q}_5$ as m varies. Indeed for the parameters $r_P = 15$, $r_T = 10$, $K = 180$, $H = 100$, $k = 0.04$, $h = 0.04$, $a = 100$, $b = 500$, $c = 1.5$, $g = 1$, $e = 1$, $\rho = 0.5$, $m = 3$ we find $\widetilde{Q}_6\,(55.06;4.1;42.5)$ and $\widetilde{Q}_5\,(163.37;3.26;0)$. The eigenvalues for these two equilibria are respectively

$$\lambda_{1,2} = -1.2 \pm 7.8,\ \lambda_3 = -7.4; \qquad \lambda_1 = -14.44,\ \lambda_2 = -2.64,\ \lambda_3 = 17.77.$$

The coexistence equilibrium is stable, while $\widetilde{Q}_5$ is unstable, Fig. 11, while taking a larger value for the bifurcation parameter, namely $m = 20.8$, $\widetilde{Q}_6$ becomes unstable and Q_5 stable, see Fig. 12.

In addition to the previously found coexistence equilibrium and zooplankton-free equilibrium, for the same set of parameter values also another

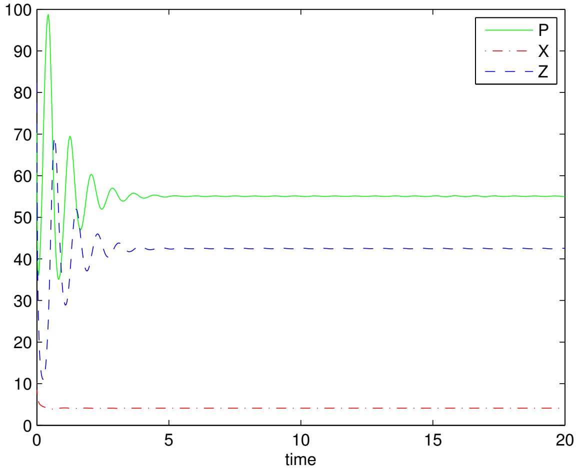

Figure 11. $\widetilde{Q}_6$ stable with $r_P = 15$, $r_T = 10$, $K = 180$, $H = 100$, $k = 0.04$, $h = 0.04$, $a = 100$, $b = 500$, $c = 1.5$, $g = 1$, $e = 1$, $\rho = 0.5$, $m = 3$.

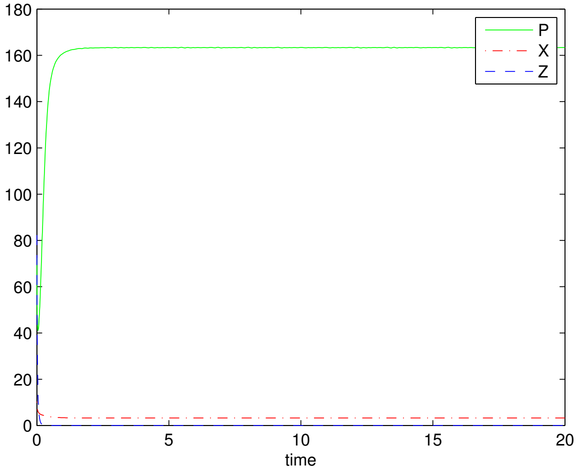

Figure 12. $\widetilde{Q}_6$ becomes unstable and $\widetilde{Q}_5$ stable for the same parameter values as Fig. 11 but with $m = 20.8$.

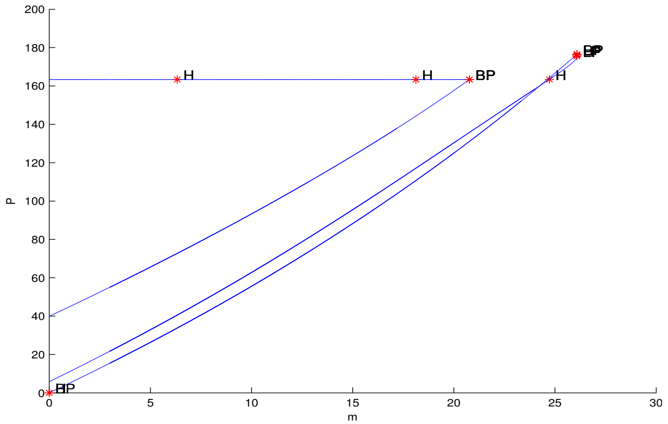

Figure 13. The P-component of the equilibrium points are plotted against m to show the bifurcations.

pair exists, $E_{1*}(21.728, 2.256, 66.417)$ and $E_2(15.464, 0, 70.677)$. These two pairs of points undergo some bifurcations which are shown in Fig. 13 as functions of the parameter m.

$\widetilde{Q}_6$ collides with $\widetilde{Q}_5$ when $m = 26.092$ and we find a branch point (BP), i.e. a transcritical bifurcation. In the bifurcation diagram two more points are depicted on the P-component of E_1, labeled by “H”; these two points represent neutral saddles. On the other hand the equilibrium E_{1*} collides with the boundary equilibrium point E_2 at a branch point when $m = 20.777$, another transcritical bifurcation. It is interesting to note that both interior equilibrium points are not changing their stability property through Hopf bifurcation. E_{1*} is a neutral saddle when $m = 24.72$, point denoted by “H”. Observe that the notation does not correspond to a Hopf bifurcation point.

7. Models Comparison

On comparing the results of the three models, we find a positive feature, the fact that the ecosystem never disappears, since the origin is always unstable in all models. This is clearly due to the logistic assumptions on the growth of the phytoplankton populations.

The regimes in which only one phytoplankton population is present are always unstable in the first two models, while in the third one they could be sustained when the interspecific competition rate h exceeds the intraspecific competition rate $r_T K^{-1}$, for the nontoxic phytoplankton-only equilibrium, and the zooplankton natural mortality rate m is larger than its food uptake $aeK(b+K)^{-1}$ at equilibrium. The very same result holds also for the toxic phytoplankton-only equilibrium, with the difference that the last condition is somewhat lessened, as in this case also the killing rate due to poison must be taken into account in the mortality term. Hence it is easier to find an ecosystem in which only toxic phytoplankton thrives than one with harmless phytoplankters.

Toxic phytoplanktons and zooplankton seem to coexist, equilibria Q_3, in all models. Feasibility is always the same independently of the model considered, under suitable conditions, (27). Stability hinges on three conditions, one of which is the same for all models and imposes an upper bound on the release of toxins, (33). For the first and third model, the population size at equilibrium of the toxic phytoplankton must be large enough, (32). Finally, the harmless phytoplankton reproduction rate must also be bounded from above, in the first and second model the bound being the very same.

The poisonous phytoplankton-free equilibrium is found again in all the models with the very same population values. For its feasibility the zooplankton natural mortality rate must not exceed the food uptake rate from grazing on the harmless phytoplankton and the population value of the latter at equilibrium must fall below the environment's carrying capacity K. While feasibility gives this lower bound on K, stability imposes on it an upper bound,

$$K < b + \frac{2bm}{ae - m}.$$

Further, the zooplankton population level at equilibrium must be large enough, for the first model (18), and two different suitable combinations of the two nonzero populations at equilibrium must be large enough for the remaining models.

The zooplankton-free equilibrium exists in all models, but in the second one it is not unique, but rather a segment of continuous equilibria. In the first model it is always feasible, in the second one feasibility specifies the range in which it can be found, in the last model it is feasible and stable if the intraspecific competition rate exceeds the interspecific one, namely

$$\frac{r_P}{k} > H, \quad \frac{r_T}{h} > K,$$

for the harmless and toxic phytoplanktons respectively. In addition the product of the intraspecific rates must be larger than the product of the interspecific ones,

$$\frac{r_P}{k}\frac{r_T}{h} > HK.$$

These are then specific feasibility and stability conditions for (60), but another one must be added for all models, stating that the zooplankton's food uptake must not exceed the whole zooplankton mortality rate, i.e. natural one plus the one due to the toxins, evaluated when the poisonous phytoplankton is at carrying capacity level.

Coexistence has been numerically verified to sussist in models (18) and (60), while we have not been able to obtain a stable equilibrium with all populations thriving for model (42). In the first model, Hopf bifurcations arise, giving rise to persistent population oscillations, when the zooplankton mortality is low enough. In the literature, the model in [25] contains Holling type II terms for the grazing of zooplankton over the two phytoplankton populations. Limit cycles are found and explored numerically in terms of the zooplankton's feeding uptake rates. In model (18) in addition another phenomenon arises, for which the unstable limit cycle originating from a subcritical Hopf bifurcation for increasing mortality rate grows larger, until at a certain threshold value of the natural zooplankton mortality it collides with a stable one, thereby turning off the planktonic blooms. This could be an important feature in practical situations, to lessen the damages of harmful algal blooms. It is also relevant to remark that in model (60), while the three populations can stably coexist, no Hopf bifurcations arise. This is not uncommon, as in the literature a system with the same populations as the ones presented here and incorporating Holling type II terms for modeling the release of poison does not seem to show recurring oscillations either, [11]. Neither the use of two toxic populations and nonlinearities of Holling type III cause the population oscillations to persist in time, [27]. Also the recently considered models including the Monod-Haldane response, for which the zooplankton avoids to feed when the toxins are released, do not exhibit persistent oscillations, [3,28]. Instead, here, transcritical bifurcations are found, from which the coexistence equilibrium originates from the zooplankton-free environment when zooplankton establishes itself persistently in the system. This occurs in all the models considered. A feature of this sort is also present in simpler models, for instance when only toxic phytoplankton and zooplankton are modeled, [10].

Persistent oscillations for the nonvanishing populations arise in the same way near the equilibria in which one of the phytoplankton populations is not present. Again, given that these equilibria are the same in the three models, this occurs independently of the model at hand. These limit cycles are thus found in subspaces of the phase space, but in a similar model with just toxic phytoplankton and zooplankton, to have persistent oscillations, delays must be introduced in the model, [26]. Alternatively, if only one population of phytoplankton is considered, which is toxin-releasing, but at the same time edible by zooplankton, also nutrients have to be explicitly considered to obtain limit cycles, [23]. The even simpler model [8], with nutrients and toxic phytoplankton but without zooplankton, shows not just persistent oscillations but even chaotic system's behavior if seasonal effects are explicitly introduced. This result is clearly obtained via the exogenous term explicitly built in via a time-varying forcing function accounting for the toxin release.

In the first of the two papers that have already used the patch hypothesis, [12], monospecies blooms have been simulated under suitable conditions, with the poison-releasing phytoplankton driving the zooplankton to extinction.

Monospecies blooms occur also in our more realistic situation, in that it incorporates also harmless phytoplankton in the model. For instance in model (18) for the following parameter values $r_P = 2$, $r_T = 8.5$, $a = 1$, $b = 5$, $c = 1$, $e = 0.8$, $g = 30$, $m = 0.2$, $H = 70000$, $K = 6$, $\rho = 0.3$, representing a particularly unfavorable environment for the harmless phytoplankton and a very good one for the toxic phytoplankton, we find that the latter overtakes the former, while zooplankton is completely wiped out, see Figure 14.

Observe finally that [13] modifies a bit the model of [12] in that the term using the Holling type II response function is replaced by a simpler bilinear nonlinearity. It goes a step beyond, however, since the model is then extended to a reaction-diffusion system, replacing the fractional power term for zooplankton toxic mortality by explicitly incorporating also space, showing that some patterns in the spatiotemporal domain arise. Similarly, in a different ecological context, alike features are discovered due to the mechanism of prey group defense, [33]. In this paper then space is explicitly dealt with, we could say at a much coarser level, retaining the group defense mechanism, i.e. the $T^{\frac{2}{3}}$ term, in the equations. In fact, the lumping mechanism for which we assume the toxic phytoplankton to aggregate in patches represents in principle a way of eliminating space from the model. This occurs however at a finer scale. Therefore, although space is once again considered explicitly in [13, 33], the

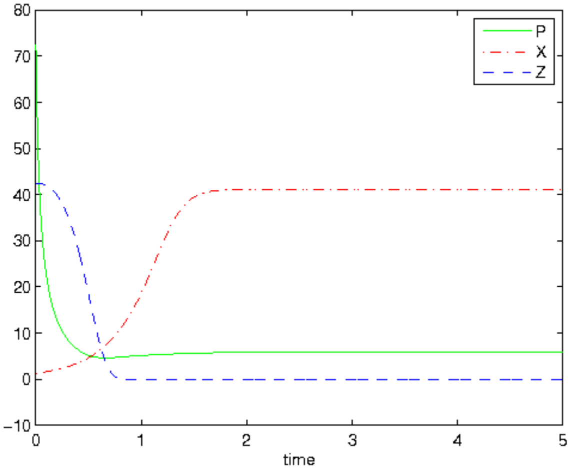

Figure 14. Model (18), exhibiting the monospecies bloom, for the parameter values $r_P = 2$, $r_T = 8.5$, $a = 1$, $b = 5$, $c = 1$, $e = 0.8$, $g = 30$, $m = 0.2$, $H = 70000$, $K = 6$, $\rho = 0.3$.

reaction-diffusion equations used in the model differ from the ones classically used, [22].

These represent further and exciting areas that open up new lines of investigation. We do not pursue them here, but leave them for possible future research efforts.

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Chapter 3

THEMATIC MAPS, A TOOL TO ESTABLISH THE SPATIAL PATTERNS OF EUTROPHICATION AND THE ZOOPLANKTON COMMUNITY STRUCTURE IN A TROPICAL URBAN RESERVOIR (PAMPULHA RESERVOIR, MG) IN BRAZIL

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ABSTRACT

In this chapter we evaluated the effect of inputs of nutrients, mainly nitrogen and phosphorus, on the structure of the zooplankton community, including diversity, evenness, dominance and richness, in Pampulha

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Reservoir in the city of Belo Horizonte, Brazil. The samples were taken on 15 September 2009 at 23 sampling stations, covering the entire reservoir. A spatial analysis showed that the species richness gradually decreased in those sites where increased nutrients and several highly opportunistic species increased in density along this same spatial gradient (such as *Thermocyclops decipiens*, *Metacyclops mendocinus* and *Brachionus calyciflorus*). Thematic maps describing the horizontal distribution of each variable showed that areas with higher nutrient concentrations were associated with increases in dominance and decreases in diversity and species richness. Finally, establishing the horizontal distribution patterns of zooplankton organisms in a reservoir allow us to perform a detailed ecological zonation of the water body and one of the most interesting applications of this zonation is the identification of ecological gradients related to pollution sources.

Keywords: Brazil, diversity, eutrophication, nutrients, tropical reservoir, zooplankton, Pampulha reservoir, thematic maps

INTRODUCTION

Zooplankton has long been used as an indicator of water quality in lakes (Gannon and Stemberger, 1978; Bays and Crisman, 1982; Pejler, 1983; Pinto-Coelho et al., 2005b). Nonetheless, variable responses of zooplankton to trophic status are common (Ravera, 1996), perhaps in part because zooplankton also respond to other environmental factors such as lake water chemistry (Pinel-Alloul et al., 1990; Hulot et al., 2000), shoreline disturbances and watershed land use (Stemberger and Lazorchak, 1994; Pinto-Coelho, 1998; Patoine et al., 2000), as well as levels of vertebrate and invertebrate predation (Hanazato and Yasuno, 1989; Walls et al., 1990).

Brazil has an immense richness of freshwater ecosystems. Nevertheless, this country is facing a dramatic shift in the water quality of several important systems, caused by a variety of human impacts: dam construction, erosion and silting, eutrophication, contamination with metals and Persistent Organic Pollutants-POPs, habitat fragmentation, introduction of alien species, etc. (Pinto-Coelho, 1998; Torres et al., 2007; Tundisi and Matsumura-Tundisi, 2008).

One of the major human-induced changes in aquatic environments is eutrophication, usually caused by excessive nutrient external inputs. Eutrophication has dramatically affected phytoplankton biomass and community structure in lakes (Anneville and Pelletier, 2000; Dokulil and

Teubner, 2005). Eutrophication effects often propagate up to higher trophic levels resulting in changes to the zooplankton community (Ravera, 1980; Lovik and Kjelliberg, 2003; Anneville et al., 2007). It is expected that eutrophication affects several aspects of community structure such as density, richness, diversity, evenness and dominance. Specifically in Pampulha Reservoir, these changes may result in the exclusion of some species such as *Bosmina longirostris, B. hagmanni* and *Scolodiaptomus cordeoi* and increased population growth of others such as *Thermocyclops decipiens*, *Metacyclops mendocinus* and *Brachionus calyciflorus* (Pinto-Coelho, 2012).

Eutrophication of the Pampulha Reservoir was initially detected and characterized by Giani et al. (1988). Since then, several studies have demonstrated the continuous intensification of eutrophic conditions in the reservoir, which has caused recurrent cyanobacteria blooms and outbreaks of aquatic macrophytes (Pinto-Coelho, 1998; Pinto-Coelho and Greco, 1999; Greco and Freitas, 2002; Torres et al., 2007; Pinto-Coelho, 2012). Here, we examined the effect of the nutrient input, mainly nitrogen and phosphorus on structural attributes of the zooplankton community, including diversity, evenness, dominance and richness, during a sampling campaign. We used a series of thematic maps describing the horizontal distribution of some variables evaluated to examine whether areas with higher nutrient concentrations are associated with increases in dominance and decreases in diversity and species richness.

STUDY AREA

Pampulha Reservoir is located in the northern part (43°56′47″W; 19°55′09″S) of the city of Belo Horizonte, capital of the state of Minas Gerais, Brazil. This is a small lake constructed in 1938, intended as a recreational area and also a drinking-water supply. However, the water treatment plant was closed in 1980 because of frequent blooms of blue-green algae, and large areas of the lake have been lost due to silting. Initially, Pampulha Reservoir had a surface area of 2.1 km^2 and a volume of 12 million m^3 (Pinto-Coelho et al., 2005a). The architectural complex around the reservoir is a major tourist area for the city, but uncontrolled occupation of the basin has caused extensive environmental deterioration of this waterbody, mainly accelerated eutrophication and decreased depth (Araújo and Pinto-Coelho, 1998). The silting process led to reduction of more than 15 % in lake’s area and a 23 % decrease in its volume (Resck et al., 2008). As a result, the reservoir presently has a total surface of only 1.8 km^2 and a volume of 9.2 million m^3. The maximum depth decreased from 17 to 15.1 m, and the mean depth is now 4.98 m (Pinto-Coelho, 2012).

A previous investigation examined the basic temporal patterns of seasonal evolution of water quality in this reservoir (Giani et al., 1988). According to this seasonal pattern, the most critical environmental conditions are typically observed during the dry season, which usually extends from May to September.

WATER SAMPLE COLLECTION

The samples were taken subsurface (0.5 m depth) between 10:00 and 17:00 hs on 15 September 2009 at 23 sampling stations, covering the entire reservoir (Figure 1). At each station, depth, water transparency (Secchi disk), chlorophyll *a* (Fluorimetric Sonde Turner/SCUFA) and water temperature, dissolved oxygen and electrical conductivity (Yellow Springs Instruments-YSI multi-parameter probe, model 556) were measured *in situ*. Subsurface (0.5 m depth) water samples were collected in 5-liter plastic containers for measuring turbidity (DIGIMED model M-3), total solids (gravimetric; Clesceri et al., 1998), total organic nitrogen (semi-micro Kjeldahl; Clesceri et al., 1998) and phosphorus (reaction with ascorbic acid; Clesceri et al., 1998), ammonium, nitrites and nitrates were measured followed Mackereth et al. (1978) in the laboratory. Previous investigations (Giani et al., 1988; Pinto-Coelho, 1998) have demonstrated that most biological and chemical properties of this reservoir are rather homogeneous during the dry season, usually May through late October.

Zooplankton was collected at each station with bottom to surface vertical hauls of a plankton net (30 cm diameter and 68 μm mesh). The organisms were preserved with 4 % buffered formalin and transported to the Laboratory of Environmental Management of Reservoirs of the Biological Sciences Institute at the Universidade Federal de Minas Gerais for identifying and counting. Zooplankton was identified mostly to species by means of taxonomic keys by Koste (1978), Sendacz and Kubo (1982), Reid (1985), Zoppi de Roa et al. (1985), Koste and Shiel (1987), Elmoor-Loureiro (1997) and Fernando (2002). Zooplankton specimens were counted in a Sedgwick-Rafter chamber with 1.0 mL capacity. Aliquots of 1.0 mL were counted fully to complete at least 400 individuals in each sample, to ensure accuracy not lower than 90 % (Edmonson and Winberg, 1971; McCauley, 1984; Pace, 1986). The density was reported in organisms per liter. We used a Leica DMLB microscope at 100x magnification, equipped with a video camera (Sony CCD Video CAM) and image-processing software (SIGMASCAN® Systat Software Inc.). Using the zooplankton density data, we calculated the community-structure indices: Richness as the number of species, Diversity (Shannon and Weaver, 1949), Dominance (Simpson, 1949) and Evenness (Pielou, 1975), with the PAST statistical program (Hammer et al., 2001). For details about how each index was calculated see Hammer et al. (2001).

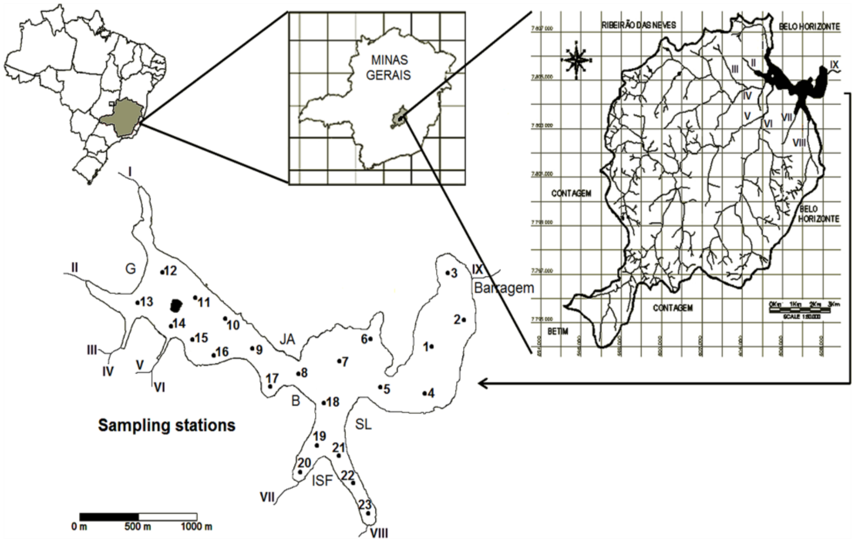


Figure 1. Location of the Pampulha Reservoir and its drainage basin (Streams: I. Olhos d'Água; II. AABB; III. Baraúna; IV. Água Funda; V. Sarandi; VI. Ressaca; VII. Tijuco; VIII. Mergulhão; IX. Effluent. Sectors: JA. Jardim Atlântico; G. Garças; B. Bandeirantes; ISF. Igreja de São Fancisco de Assis; SL. São Luis) and of the 23 sampling stations (the black area within the reservoir accounts for Amores Island).

For each variable we calculated the mean as a measure of central tendency, standard deviation as a measure of absolute dispersion, and Pearson variation coefficient as a measure of relative dispersion. Relationships between variables were established with Pearson Correlation Coefficient, with the program STATGRAPHICS Plus 5.1® (Statistical Graphics Corp.). The trends between stations for physical and chemical variables, densities and community structure evaluators of zooplankton assemblage were explored by Principal Component Analysis (PCA). The data matrix was formed by 23 cases (sampling points) and 20 variables collected at surface (z= 0.5 m), on 15

September 2009 in Pampulha Reservoir, Belo Horizonte. All data variables were ln-transformed ($xt = \ln(x+1)$) prior to the analysis. The rotation procedure VARIMAX was used. No resampling was considered. The correlation matrix for extraction was used. Only the first two axes were considered since they host the bulk of total variability (70 %). The software SYSTAT version 11 for Windows 7.0 was used (Licence: LGAR-FUNDEP-UFMG).

The thematic maps of the horizontal variation of the variables were obtained using the program Surfer 9.0® (Golden Software Inc.), and the kriging interpolation method. The reservoir shoreline was digitized with the program Didger 3.0® (Golden Software Inc.) from a high-resolution image of the Pampulha Reservoir obtained from Google Earth Pro® (Google Inc.). After digitalization, the image was geo-referenced with nine neighboring control points with high-precision coordinates (error < 0.05 m) using DGPS GTR-A® (TechGeo Ltda.).

ZOOPLANKTON VARIABILITY AND INTERRELATION WITH THE ENVIRONMENT

The water temperature and the electrical conductivity were the variables that presented greater stability (their coefficients of variation were lower than 7 %). Similarly, chlorophyll *a* and dissolved oxygen showed low coefficients of variation (17.6 and 27.1 % respectively). The other variables showed high fluctuations all over the reservoir (CV> 43 %).

The coefficients of variation for the nutrients were above 43 % and, overall, the nitrogen concentration was 6 to 53 times higher than the phosphorus concentration. For the community attributes, the coefficients of variation were low and generally close to 27 %. The densities of all zooplankton groups varied widely, with coefficients of variation of 99 % or higher in all cases (Table 1).

Nutrients (specifically Total Nitrogen and Total Phosphorus) showed negative correlations with Diversity and Richness of species, and positive with Dominance. Electrical conductivity was positively correlated with Richness of species and Total Phosphorus. Chlorophyll *a* was positively correlated with Dominance and Total Nitrogen, and negatively correlated with Diversity and Evenness (Table 2).

Table 1. Exploratory basic statistical analysis for the abiotic and biotic variables measured at 23 sampling stations in the Pampulha Reservoir. CV % accounts for Pearson variation coefficient.

Variables	Min.	Max.	Mean	SD	CV%
Water temperature (°C)	22.7	28.5	26.1	1.68	6.5
Transparency (m)	0.1	1.0	0.4	0.23	55.7
Electrical Conductivity (μS/cm)	385	470	411.9	28.13	6.8
Dissolved oxygen (mg/L)	5.2	14.5	8.4	2.27	27.1
Chlorophyll *a* (μg/L)	38.7	70.0	53.5	9.39	17.6
Turbidity (NTU)	24.8	421.0	147.2	101.48	68.9
Total solids (mg/L)	19.7	188.4	68.0	41.24	60.7
Total nitrogen (mg/L)	1.1	18.0	7.0	3.85	53.8
Nitrate (mg/L)	0.05	10.1	4.2	3.47	82.6
Nitrite (mg/L)	0.05	0.8	0.5	0.23	45.4
Ammonium (mg/L)	1.7	5.6	2.6	1.15	43.7
Total phosphorus (mg/L)	0.1	1.2	0.4	0.22	62.4
N:P Ratio	6.0	53.4	22.1	11.99	54.2
Diversity (H′)	1.30	2.17	1.8	0.22	12.0
Evenness (J′)	0.54	0.84	0.7	0.07	9.7
Dominance (Ds)	0.14	0.37	0.2	0.06	27.3
Species richness (S)	10.0	16.0	12.7	2.05	16.1
Density of Copepods (org/L)	119.1	4911.9	694.9	988.95	142.3
Density of Rotifers (org/L)	10.3	288.6	91.8	91.73	99.9
Density of Cladocerans (org/L)	15.1	325.4	59.7	69.78	117.0
Density of Ostracods (org/L)	11.3	260.3	68.6	72.66	105.9

Table 2. Variables with statistically significant correlations ($p < 0.05$)

VARIABLES	r	p
Total Nitrogen-Chlorophyll *a*	0.44	0.0348
Total Nitrogen-Diversity	-0.53	0.0095
Total Nitrogen-Dominance	0.48	0.0197
Total Nitrogen-Species richness	-0.51	0.0119
Total Phosphorus-Electrical Conductivity	0.69	0.0003
Total Phosphorus-Diversity	-0.52	0.0108
Total Phosphorus-Dominance	0.49	0.0186
Total Phosphorus-Species richness	-0.60	0.0025
Electrical Conductivity-Species richness	0.60	0.0025
Chlorophyll *a*-Diversity	-0.58	0.0036
Chlorophyll *a*-Evenness	-0.59	0.0031
Chlorophyll *a*-Dominance	0.58	0.0038

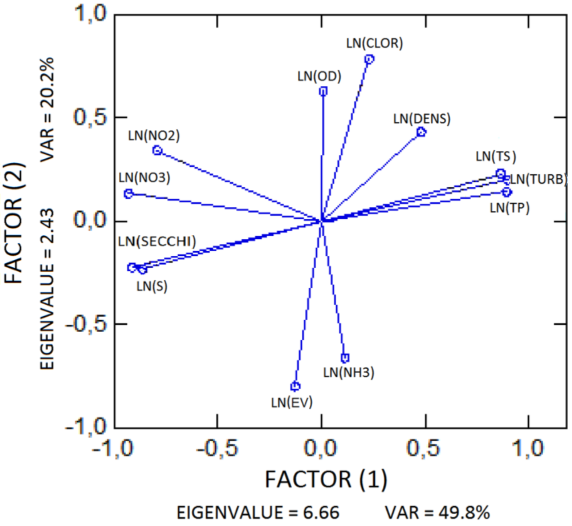
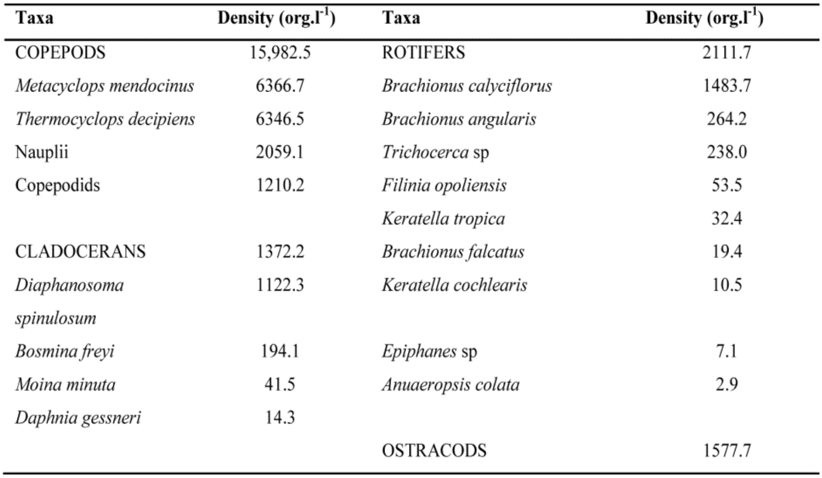


Figure 2. Biplot diagram showing the results of PCA for environmental variables (NO2: nitrite, NO3: nitrate, SECCHI: water transparency, NH3: ammonium, CLOR: chlorophyll *a*, OD: dissolved oxygen, TS: total solids, TURB: turbidity, TP: total phosphorus). The biotic variables refer to zooplankton community descriptors (EV: species evenness, S: species richness, DENS: density). The symbols LN before each variable indicate that they are ln-transformed prior to PCA analysis.

The composition of zooplankton assemblages in Pampulha Reservoir is shown in Table 3. A total of 16 taxa were found, the highest species richness was for the rotifers group with 7 species and two morphospecies. However rotifers only accounted for 10.1 % of the total density, and *Brachionus calyciflorus* was the species with the highest density. We also found four species of cladocerans which account for 6.5 % of the total density; the most abundant species was *Diaphanosoma spinulosum*. There was a morphospecies of ostracods, and finally the copepods were the group with the highest densities (75.9% of total) represented by *Metacyclops mendocinus* and *Thermocyclops decipiens*.

Table 3. Total density (org.l^{-1}) of zooplankton collected in the Pampulha Reservoir



Taxa	Density (org.l^{-1})	Taxa	Density (org.l^{-1})
COPEPODS	15,982.5	ROTIFERS	2111.7
Metacyclops mendocinus	6366.7	*Brachionus calyciflorus*	1483.7
Thermocyclops decipiens	6346.5	*Brachionus angularis*	264.2
Nauplii	2059.1	*Trichocerca* sp	238.0
Copepodids	1210.2	*Filinia opoliensis*	53.5
		Keratella tropica	32.4
CLADOCERANS	1372.2	*Brachionus falcatus*	19.4
Diaphanosoma spinulosum	1122.3	*Keratella cochlearis*	10.5
Bosmina freyi	194.1	*Epiphanes* sp	7.1
Moina minuta	41.5	*Anuaeropsis colata*	2.9
Daphnia gessneri	14.3		
		OSTRACODS	1577.7

Figure 2 shows the biplot diagram with the results of PCA for environmental and biotic variables as refer to zooplankton community descriptors. The total variance explained by the first two components was 70 %. For the first axis the variance was 49.8 % while for the second axis it was 20.2 %. The PCA factor 1 was able to describe well important zooplankton community species structure descriptors, such as total density and total species richness. The PCA showed clearly that the total zooplankton species richness was associated to water transparency. Conversely, total density of zooplankton was associated to variables such as total solids and turbidity. Factor 2 was able to show the expected association between chlorophyll *a* and dissolved oxygen and this factor also showed an association between zooplankton evenness and ammonium.

The thematic maps illustrate the horizontal distribution of the different variables: water temperature, total solids, water transparency and electrical conductivity (Figure 3), the dissolved oxygen, chlorophyll *a* and nutrients (Figure 4), the densities of the main zooplankton groups collected (Figure 5), and the community structure indexes (Figure 6).

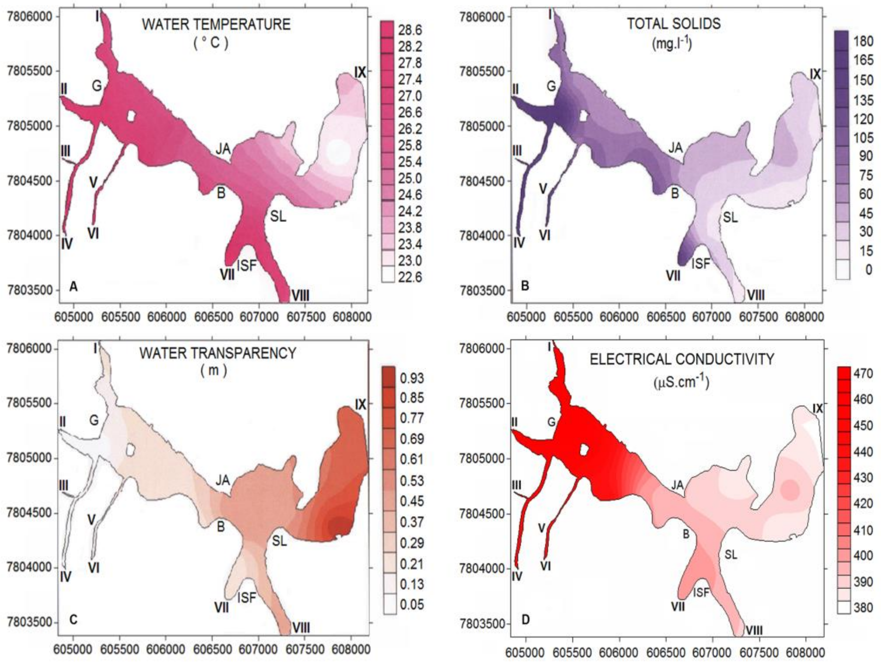


Figure 3. Thematic maps of the horizontal distribution of principal physical and chemical variables in the Pampulha Reservoir. (streams: I. Olhos d'Água; II. AABB; III. Baraúna; IV. Água Funda; V. Sarandi; VI. Ressaca; VII. Tijuco; VIII. Mergulhão; IX. Effluent. Sectors: JA. Jardim Atlântico; G. Garças; B. Bandeirantes; ISF. Igreja de São Fancisco de Assis; SL. São Luis. The white area within the reservoir accounts for Amores Island).

The water temperature generally presented high values in all locations and showed a gradual increase from the deeper compartment toward the shallower region of the dam around the Amores Island (Figure 3A). The water transparency was low in the entire reservoir, the lowest values being found in shallower stations in proximity to Amores Island (Figure 3C), and was on these same stations where they were found the highest values for total solids

(Figure 3B). The electrical conductivity showed high values all over the reservoir, and marked spatial gradient, characterized by an increase in its values towards the shallower compartment of the reservoir (Figure 3D).

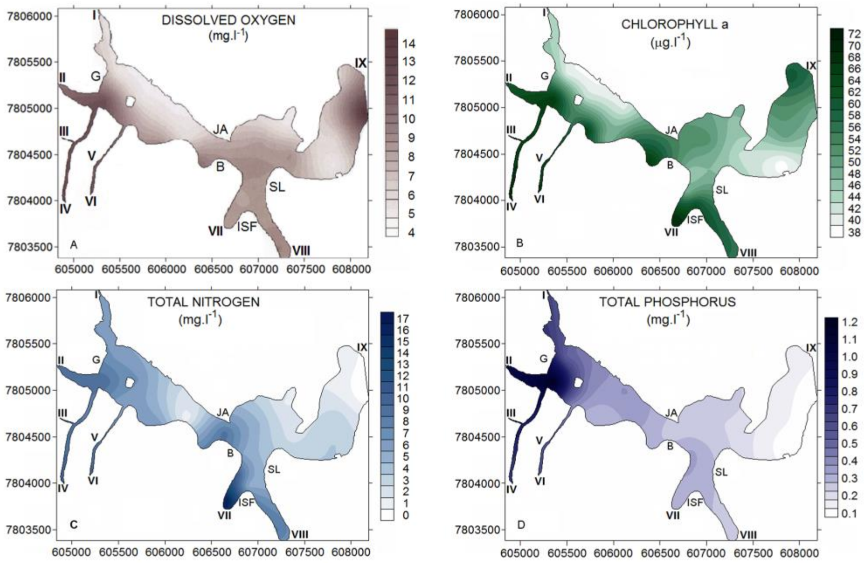


Figure 4. Thematic maps of the horizontal distribution of dissolved oxygen, chlorophyll *a* and principal nutrients, in the Pampulha Reservoir. (streams: I. Olhos d’Água; II. AABB; III. Baraúna; IV. Água Funda; V. Sarandi; VI. Ressaca; VII. Tijuco; VIII. Mergulhão; IX. Effluent. Sectors: JA. Jardim Atlântico; G. Garças; B. Bandeirantes; ISF. Igreja de São Fancisco de Assis; SL. São Luis. The white area within the reservoir accounts for Amores Island).

Elevated values of dissolved oxygen were found to the Garças sector at the mouths of AABB, at Baraúna and Água Funda streams and around the Amores Island (Figure 4A) Also, high chlorophyll *a* concentrations were recorded at the mouths of AABB, Baraúna and Água Funda streams and the area near the Igreja de São Fancisco de Assis, at the confluence of the Tijuco and Mergulhão streams (Figure 4B). The highest concentrations of the principal nutrients were found in the shallow areas of the reservoir, mainly around Amores Island. Total Nitrogen was highest near the mouth of Tijuco stream and also near the Garças sector at the mouths of AABB, Baraúna and Água Funda streams (Figure 4C), while total phosphorus concentrations were higher at the mouths of AABB, Baraúna, Água Funda, Sarandi and Ressaca streams (Figure 4C).

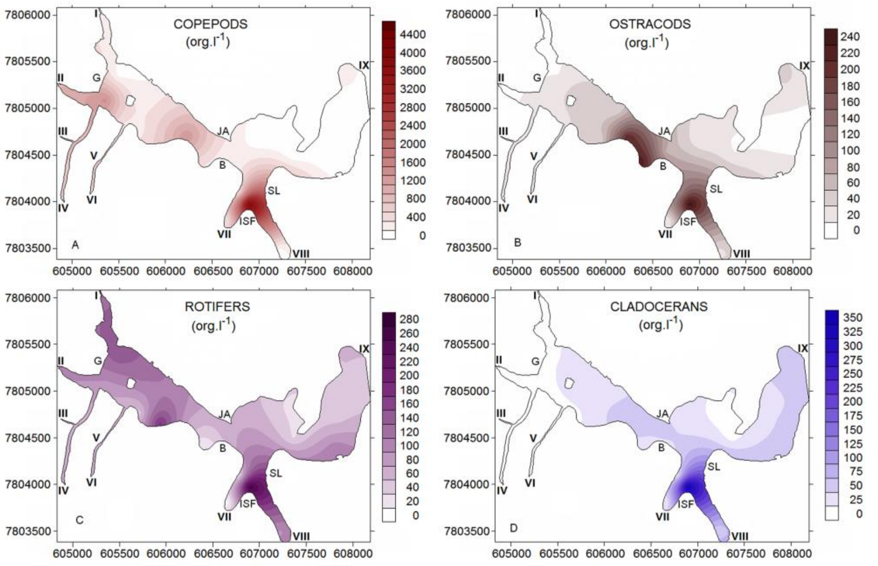


Figure 5. Thematic maps of the horizontal distribution of the main zooplankton groups in the Pampulha Reservoir. (streams: I. Olhos d’Água; II. AABB; III. Baraúna; IV. Água Funda; V. Sarandi; VI. Ressaca; VII. Tijuco; VIII. Mergulhão; IX. Effluent. Sectors: JA. Jardim Atlântico; G. Garças; B. Bandeirantes; ISF. Igreja de São Fancisco de Assis; SL. São Luis. The white area within the reservoir accounts for Amores Island).

Copepods (Figure 5A) showed the highest density, the adult forms were concentrated mainly in the area near the Igreja de São Fancisco de Assis, at the confluence of the Tijuco and Mergulhão streams, whilst the immature forms were placed into shallower areas, mainly around the Amores Island. The ostracods (Figure 5B) were concentrated near the Igreja de São Fancisco de Assis and the Bandeirantes sector. Rotifers (Figure 5C), were abundant mainly in the shallow areas of the reservoir around the Amores Island and near the Igreja de São Fancisco de Assis sector, and lastly, higher abundance values of the cladocerans (Figure 5D) was recorded near the Igreja de São Fancisco de Assis, at the confluence of Tijuco and Mergulhão streams.

The highest values for Richness (Figure 6A) were found in the deeper areas, mainly toward the dam area, near the outflow. Diversity (Figure 6B) was highest near Amores Island and the dam area. The highest values of Dominance (Figure 6C) were found at the mouth of Tijuco stream near the Igreja de São Fancisco de Assis and the mouths of AABB, Baraúna and Água

Funda streams, and finally the Evenness (Figure 6D) was highest around Amores Island, and at the mouth of Mergulhão streams.

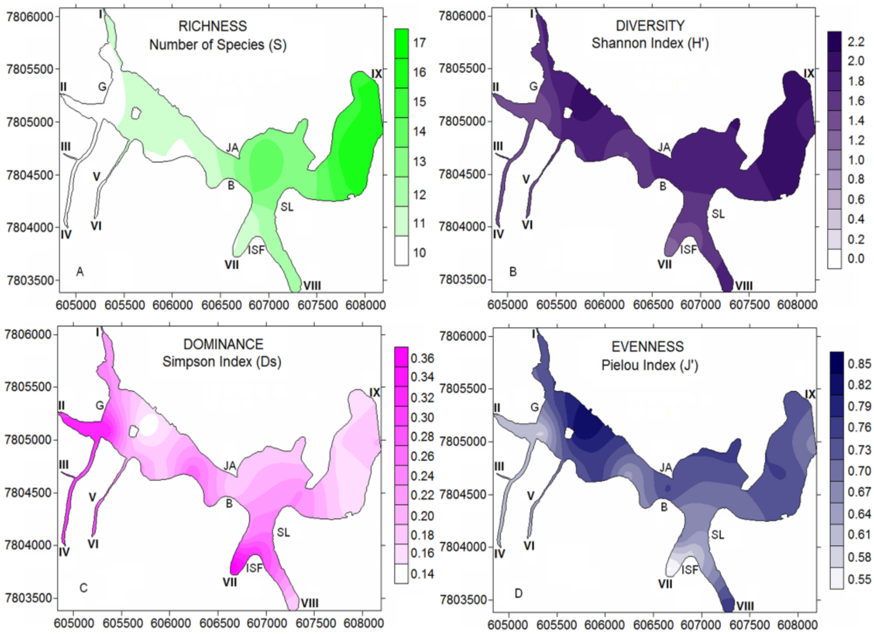


Figure 6. Thematic maps of the horizontal distribution of the zooplankton community structure indices in the Pampulha Reservoir. (streams: I. Olhos d'Água; II. AABB; III. Baraúna; IV. Água Funda; V. Sarandi; VI. Ressaca; VII. Tijuco; VIII. Mergulhão; IX. Effluent. Sectors: JA. Jardim Atlântico; G. Garças; B. Bandeirantes; ISF. Igreja de São Fancisco de Assis; SL. São Luis. The white area within the reservoir accounts for Amores Island).

CONCLUSION

Water temperature plays a fundamental role regulating numerous physical and chemical processes that take place in aquatic ecosystems, however, the tropical ecosystems show, as a general characteristic, a high thermal uniformity, which was reflected in the low variation coefficient of this variable.

Pampulha Reservoir has low levels of water transparency the lowest values were recorded in the shallower stations, suggesting that this decrease may be caused by resuspension of bottom sediments, as a result of the action of wind over the water surface. This process is able to create a mixing zone that can influence the entire the water column, a situation that is also reflected in the variation of the total solids, which also presented the highest concentrations in more shallow sites.

Another characteristic of eutrophic reservoirs, as Pampulha, is the occurrence of high levels of oxygen in the shallow stations during the warmest and sunny hours of the day. These high oxygen concentrations were coupled with the highest concentrations of chlorophyll *a* at the same stations of the reservoir.

The nitrogen and phosphorus concentrations are typical of a highly eutrophic environment (Tundisi and Matsumura-Tundisi, 2008). Nitrogen, along with phosphorus, is of the most influential macronutrients in the eutrophication of lakes, rivers and reservoirs. Its main inorganic forms are the ammonium, as well as nitrite and nitrate ions. In the Pampulha Reservoir all forms of inorganic nitrogen were found in high concentrations and its spatial pattern is directly associated with contaminated water discharges, since the highest concentrations were found in the areas near the mouths of Tijuco and Mergulhão streams, which are canalized and covered. This coverage prevents the entry of light, and apparently favors the processes which increase the concentration of nitrogen forms in the water.

The above results show a clear spatial pattern of trophy in the reservoir. The trophic condition usually increases from the dam to the reservoir arm, which have tributaries of various sizes, or near to Amores Island where inputs from several polluted tributaries grouped into an artificial concentration canal. Most physical, chemical and biological variables being important in the eutrophication including conductivity, phosphorus, nitrogen and chlorophyll *a*, usually follow this spatial pattern. Different studies have shown that the Pampulha Reservoir functions as a nutrient trap (Torres et al., 2007; Pinto-Coelho, 2012) and specifically a great amount of phosphorus is retained in different compartments of biota and sediments. These studies have shown that Sarandi and Ressaca rivers are primarily responsible for the greatest contributions of phosphorus reaching the reservoir.

One of the most important ecological theories is the theory of biodiversity (Hubbell, 2001), which states that heavily impacted ecosystems will undergo large and conspicuous structural as well as functional modifications. Among the most notorious effects of pollution and other forms of human impact, are the loss of species and the increase in dominance of a few opportunistic organisms (Johnston and Roberts, 2009). Although these approaches are generally accepted, few reports have clearly associated eutrophication with the structural properties of tropical plankton communities on a spatial basis (Tundisi and Matsumura-Tundisi, 2008).

The ultimate causes of this phenomenon are well known, as are the general guidelines for managing or mitigating eutrophication (WWAP, 2009). However, many questions are completely untouched and answering them requires a series of innovative investigations. Examples of such questions are: (a) For a known nutrient input, what is the timing and magnitude of eutrophication in a given system? (b) Why do the first signs of eutrophication vary from one system to another similar system? (c) Is there a general and recurrent pattern of these signals in time and space? The obvious failure to adjust to or to combat eutrophication in many parts of the world may be due not only to increased external nutrient loads, but also to the lack of quantitative knowledge related to these still-open questions regarding the response of a lake or reservoir to eutrophication. It is clear that the science of limnology must provide new tools to refine monitoring procedures. This new approach will open a series of new perspectives for the decision-making process.

The data for Pampulha Reservoir corroborates that eutrophication causes most, if not all the effects predicted by the biodiversity theory. A spatial analysis allowed us to establish that the structure of the zooplankton community followed two basic principles of general biodiversity theory: (a) species richness decreased along a spatial gradient of nutrients; (b) several highly opportunistic organisms increased in dominance along the same spatial gradient. Nevertheless, the Shannon Diversity Index showed no clear spatial pattern associated with lake's trophy.

The Pampulha Reservoir has three different compartments. The first is the shallowest area, the silted area around Amores Island. It is strongly influenced by inputs from the heavily polluted Sarandi and Ressaca rivers and to a lesser extent by Olhos d'Água, AABB, Baraúna, and Água Funda streams. This area has higher concentrations of nutrients and turbidity and increased biological productivity. The second area is the deeper middle reservoir, extending from the broader lake surface to the dam. This region has cleaner water and lower densities of algae despite discharges from Tijuco and Mergulhão streams. The third area is an intermediate zone located between Bandeirantes and Jardim Atlântico sectors, with particular conditions that show transitions between the two opposite zones.

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Chapter 4

ZOOPLANKTON VARIATION IN FIVE GREEK LAKES

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ABSTRACT

Zooplankton is an important element of the structure and function of freshwater lake ecosystems, while the study of changes in abundance, species diversity and composition in zooplankton communities can provide important indications of long term environmental changes. The present study provides elements on the community structure, the spatial and seasonal variation and the relation of zooplankton to environmental parameters in four natural lakes (Trichonis, Amvrakia, Lysimachia and Ozeros) and one reservoir (Stratos) situated in western Greece. Zooplankton surveys of 12 to 24 months were conducted between 2003 and 2010, while at the same time the most important physicochemical parameters were recorded. The number of species in the five lakes varied between 25 (Ozeros) and 36 (Lysimachia). The general similarities in species composition in the five lakes can be attributed to their common geological origin, while differences among them are ought either to geographical isolation, to the particular water chemistry, or to their

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trophic state. The group of copepods, and especially the calanoid *Eudiaptomus drieschi*, dominated the zooplankton community in the oligotrophic Trichonis Lake, the oligo-mesotrophic Amvrakia Lake and the meso- eutrophic Ozeros Lake. Instead, the group of rotifers dominated in the eutrophic Lysimachia Lake and in Stratos reservoir. The cladoceran species presented clear seasonal dominance succession patterns, with *Bosmina longirostris* and *Diaphanosoma orghidani* occupying the greatest percentage in winter and summer months, respectively. The larvae of the mollusk *Dreissena blanci* were important constituent on the zooplankton community in most of the lakes, except Lysimachia. In the deep lakes Trichonis and Amvrakia, the higher zooplankton density was recorded in the surface 0–20 m layer and was decreasing with depth, while small numbers of zooplankton specimens were found also in the hypoxic/anoxic hypolimnion of the latter lake. The vertical separation of the numerically most important species of crustaceans and rotifers is attributed possibly to the reduction of intra- and inter-specific competition. Temperature was the most important environmental parameter for most of the species variation, while other elements like dissolved oxygen, water level fluctuation, conductivity, chlorophyll-a and nutrients concentration played also important role in the zooplankton spatial and temporal distribution in the five lakes.

INTRODUCTION

Zooplankton organisms are important elements of the structure and function of freshwater lake ecosystems as they occupy the centre of the aquatic food web, being important as food for almost all freshwater fish at some stage in their life history, while at the same time grazing on algae, bacteria, protozoa and other invertebrates (Lampert and Sommer, 1997). Moreover, zooplankton communities are sensitive to anthropogenic impacts and their study may be useful in the prediction of long term changes in lake ecosystems (Ferrara et al., 2002; Preston and Rusak 2010), as these communities are highly sensitive to environmental variation. (Jeppesen et al., 2011). Changes in zooplankton abundance, species diversity and community composition can provide important indications of environmental change or disturbance and several studies have shown its usefulness as an indicator of changes in trophic dynamics and the ecological state of lakes related to changes in nutrient loading and climate (Caroni and Irvine, 2010; Jeppesen et al., 2011).

Although many studies have been conducted in several lakes worldwide, multiscale, spatial and temporal relationships between zooplankton variability and environmental heterogeneity are still not satisfactorily understood, due to the complexity of the different aquatic ecosystems (considering both biotic and abiotic elements), along with the global climate change (Preston and Rusak, 2010; Huber et al., 2010). Thus, it is important to investigate the main factors that may govern the biology and ecology of these organisms especially in particular freshwater ecosystems, in order to have a better possibility to predict future changes, which might influence the biodiversity worldwide. Most of the freshwater zooplankton studies in Europe have been conducted in northern lakes and in the western Mediterranean, while there is limited number of studies in lakes of the eastern part of this region. Until recently, in Greece, there were only a few studies on this biotic elements conducted in lakes of the northern part of the country, while, although the number and extend of freshwater ecosystems is considerably greater in western Greece, there was no substantial investigation on this issue. However, during the last few years there was an effort towards the investigation of the zooplankton community along with the abiotic elements in the most important lakes of this region, which produced a number of published studies (Kehayias et al., 2004; Kehayias et al., 2008; Doulka and Kehayias, 2008; 2011; Doulka, 2010; Kehayias et al., 2012; Chalkia et al., 2012; Chalkia and Kehayias, 2013a; b; Thomatou et al., 2013; Chalkia, 2013).

Considering that, the study of the biological components of a water body can produce useful information towards its quality improvement and efficient management, the present chapter summarizes all the comprehensive information on the abundance, the community structure, the spatial and temporal distribution, as well as the possible influence of the main environmental forces on the zooplankton variation, gathered from studies in lakes of western Greece in nearly a decade.

THE STUDY AREA

The present study was conducted in four natural lakes and one reservoir situated in western Greece (Figure 1). Among them, Lake Trichonis is the largest natural lake in Greece, having a surface area of 98.6 km^2, a catchment area of 421 km^2 and a potential water volume of approximately 2.868 km^3 (Zacharias et al., 2002). It is a deep (Z_{max} = 57 m, Z_{mean} = 29 m) and warm monomictic lake, exhibiting a long period of thermal stratification and previous studies have classified it as oligotrophic to mesotrophic (Doulka, 2010). There are various surface water supplies (e.g. seasonal streams), as well as groundwater inflows (approx. 30 % of the total annual water inflows), which provide an adequate quantity of water and resulted to positive water balance (Zacharias et al., 2005). The excess of water is discharged through a sluice gate canal to the adjacent Lysimachia Lake to avoid potential flooding. Lake Trichonis has great ecological and economical importance. It has been included in the protected areas of Natura 2000 due to the priority habitat of calcareous fens (*Cladium mariscus*), and it is very rich in fish species, from which the economically most important is *Atherina boyeri* Risso, 1810 (Leonardos, 2001).

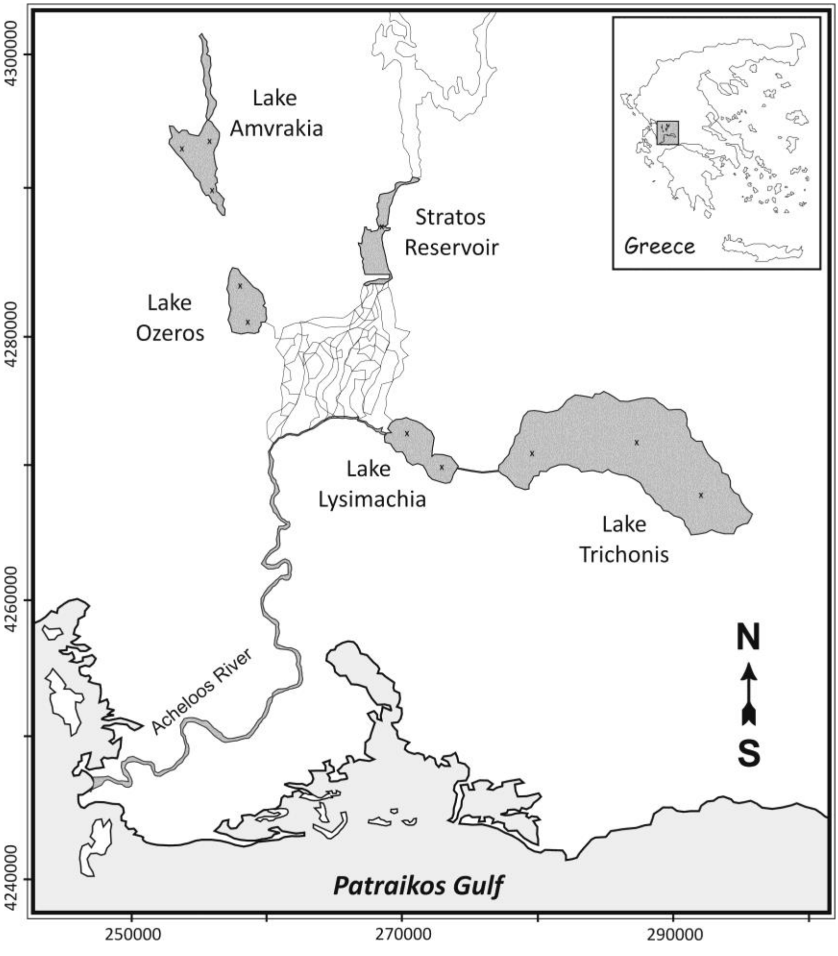


Figure 1. Geographical location of the five lakes studied. Marks (x) within each lake indicate the sampling sites.

Amvrakia is also a deep lake (Z_{max} = 50 m) with a catchment area of 112 km^2. It is a mesotrophic lake which belongs to the sulphate type (Overbeck et al., 1982). The water has high concentration of sulphates (Zacharias et al., 2002), which derive from extensive gypsum sediments especially in its western banks. The lake is supplied by water only from its drainage basin, while there are strong water level fluctuations due to high evaporation rates, especially during the summer, and the irrigation of the surrounding agricultural area. These variations usually result to the drainage of the shallower northern part of the basin (Figure 1) in certain periods/years and, consequently, to the fluctuation of the actual surface area of the lake, which on average lies between 14 and 22 km^2. The isolation of Lake Amvrakia from the other lakes of the region, along with the existing special physicochemical constants and geomorphology, has resulted to the presence of endemic species of phytoplankton (Danielidis et al., 1996).

Lake Lysimachia is a shallow lake (Z_{max} = 8.1 m), having a surface area of 13.5 km^2 and a large drainage basin of 246 km^2. It has positive water balance due to inflow of water from the nearby Trichonis Lake, with which it is connected by a sluice gate canal. Apart from various seasonal streams entering into the lake, there is also an outflow of water to Acheloos River via a canal. Until 2000, the lake was receiving the untreated urban wastes of the nearby city of Agrinio, with a population of about 80000, and thus became eutrophic. Nowadays, although Lake Lysimachia is in a better state due to the termination of the incoming of urban wastes (Chalkia and Kehayias, 2013a), it continues to receive small amounts of wastes from the surrounding agricultural areas, while also from piggeries and oil-refineries.

Lake Ozeros is also a shallow lake (Z_{max} = 5.6 m), with an area of about 10.1 km^2 and a closed drainage basin of 59 km^2 (Zacharias et al., 2002). The lake is supplied with water from seasonal streams that occur mainly in the east-southeast part, as well as from the Acheloos River, when it overflows, through a technical canal. The major environmental disturbances of Lake Ozeros are the receiving of agricultural drainage and wastes from the nearby operating farms and villages.

Finally, Stratos reservoir is the last one of four consecutive reservoirs along Acheloos River and is situated between two dams, Kastraki (upstream) and Stratos (downstream). It has a surface area of 11 km^2, its maximum depth is 15.5 m and the water volume fluctuates between 60 and 70.2 x 10^6 m^3, resulting to a mean depth between 5.5 and 6.4 m. There is poor littoral macrovegetation in the steep banks, while the human impact is not significant and restricts to agricultural and grazing (mainly sheep) activities in the surrounding area.

ZOOPLANKTON SURVEYS AND LABORATORY ANALYSIS

The present study presents the results of an extensive investigation of zooplankton in the five lakes during 2003 to 2010. In particular, zooplankton samplings have been conducted in different surveys of 12 - 24month duration (Table 1). The samplings were carried out using plankton nets with the same porosity (50 μm) but with different dimensions (length, mouth area), which were performing vertical hauls from bottom to surface. Closing nets were used in the deep lakes Trichonis and Amvrakia in order to conduct sampling in discrete depth intervals. In Lake Trichonis the zooplankton samples were taken with a conical plankton net which was manufactured to be a closing net with the addition of a second rope and a releasing trigger (Doulka, 2010). In Lake Amvrakia a Hydrobios plankton net with a closing mechanism was used. In Stratos Reservoir the sampling was conducted from a bridge crossing the reservoir (Figure 1). In all cases the nets were towed at a speed of approximately 0.5 m sec^{-1}and after the collection all samples were preserved in 4% neutralized formalin solution, in a final volume of 100 ml.

Table 1. Sampling data for the zooplankton surveys conducted in the five lakes between September 2003 and May 2010

Sampling area	Frequency / Duration	Stations / Depths	Net diameter/ porosity	Vertical hauls
Lake Amvrakia	Monthly / 24 months Sept. 2006 - Aug. 2008	Three / 45, 25, 23 m	20 cm / 50 μm	in 5 m intervals
Lake Lysimachia	Monthly / 12 months June 2009 – May 2010	Two / 8.1, 6.8 m	20 cm / 50 μm	bottom to surface
Lake Ozeros	Monthly / 12 months June 2009 – May 2010	Two / 5.6, 5.0 m	20 cm / 50 μm	bottom to surface
Lake Trichonis	Monthly / 24 months Sept. 2003 - Aug. 2005	Three / 48, 35, 25 m	40 cm / 50 μm	in 10 m intervals
Stratos Reservoir	Biweekly / 24 months Sept. 2004 - Aug. 2006	One / 8 m	40 cm / 50 μm	bottom to surface

Along with the zooplankton surveys, physicochemical parameters were measured *in situ*. Water transparency was measured in each station with a Secchi disc (diameter 30 cm), while vertical profiles of temperature, oxygen concentration, pH and conductivity were taken from the surface down to a maximum depth of 40 m, using portable instruments. For the estimation of total phosphorus (TP), phosphates (PO_4), nitrates (NO_3), nitrites (NO_2), ammonia (NH_4) and silicates (SiO_2), water samples were collected at the deepest station of the lakes from various depth intervals with a 5 L Hydrobios water sampler. Analyses of all chemical parameters were performed in the laboratory according to APHA, AWWA and WPCF (1998). For the determination of chlorophyll-a concentration (chl-a), 1500 ml of the water samples taken from the above depths was filtered through a Whatman GF/A glass fiber filter shortly after collection. Pigment extraction was made in 90 % acetone and concentrations were determined spectrophotometrically (APHA, AWWA and WPCF, 1998).

For the abundance analysis of zooplankton, three counts of 1.5 ml subsamples from each sample were made on a Sedwick-Rafter cell having a total volume of 100 ml (Doulka and Kehayias 2008). In order to have comparable data of the vertical distributions of the zooplankton groups and species, the weighted mean depth (WMD) was calculated for each taxa according to Hofmann (1975), as follows:

$$\text{WMD} = \frac{\sum(NTi \times Ti)}{\sum NTi}$$

where WMD = weighted mean depth, N_{Ti} = the abundance in the depth i, and T_i = depth (m). Although the weighted mean depth cannot represent the actual vertical distribution of a species, it is a good numerical base for the application of statistics. Thus, differences between the WMDs of zooplankton taxa were tested using the non-parametric Mann-Whitney (U-test) and the Kruskal-Wallis test ($p<0.05$). The above tests were also used for investigating differences in the environmental parameters and in the abundance of zooplankton species and groups among the sampling stations and periods.

Canonical correspondence analysis, or CCA, (Ter Braak, 1994) was used to ascertain the relationships between zooplankton and environmental variables in three of the five lakes studied (Trichonis, Amvrakia and Stratos Reservoir). The environmental variables were related to the first two axes of a direct CCA ordination performed on the zooplankton plots. The arrow direction indicates positive or negative correlations and their length is relative to the importance of the explanatory variable in the ordination.

ZOOPLANKTON COMMUNITY COMPOSITION AND GEOGRAPHIC DISTRIBUTION

The zooplankton sampling in the five lakes of western Greece during 2003 to 2010 revealed a total number of 53 invertebrate taxa which comprised four groups; 37 rotifers, 9 cladocerans, 6 copepods and one mollusc larvae (Table 2). The number of species and the community composition differed among lakes, with Lake Trichonis having the larger number of zooplankton taxa (39), followed by Lake Lysimachia (35), Lake Amvrakia (32), Stratos Reservoir (26) and Lake Ozeros (24).

Moreover, only 16 taxa were common among lakes (9 rotifers, 4 cladocerans, 2 copepods and the larvae of molluscs). In particular, the nine common rotifers were *Asplanchna priodonta* (Gosse, 1850), *Conochilus unicornis* (Rousselet, 1892), *Filinia longiseta* (Ehrenberg, 1834), *Hexarthra mira* (Hudson, 1871), *Keratella cochlearis* (Gosse, 1851), *Ploesoma hudsoni* (Imhof, 1891), *Polyarthra* sp. (Ehrenberg, 1834), *Synchaeta* sp. (Ehrenberg, 1832) and *Trichocerca similis* (Wierzejski, 1893).

The four species of cladocerans were *Bosmina longirostris* (O.F.Muller, 1785), *Ceriodaphnia pulchella* (Sars, 1862), *Daphnia cucullata* (G.O. Sars, 1862) and *Diaphanosoma orghidani* (Negrea, 1982), the two copepod species were *Eudiaptomus drieschi* (Poppe and Mrazek, 1895) and *Macrocyclops albidus* (Jurine, 1820), while the common mollusc was *Dreissena blanci* (Westerlund, 1890), from which the larvae were found in the samples. Most of the above rotifer and cladoceran species are considered common in European lakes (see in Doulka and Kehayias, 2008). Also, *E. drieschi* and *M. albidus* have been reported from lakes of the eastern Mediterranean (Apaydin Yağci, 2013).

Finally, recent studies on the biogeography of dreissenid species in southern Europe using molecular genetics found that *D. blanci* instead of *D. polymorpha* was resident in lakes of western Greece (Albrecht et al., 2007; Wilke et al., 2010), and Kehayias et al. (2012) were the first to verify the presence of this species in all the lakes of the present study.

Table 2. List of the zooplankton species found in the five lakes

ROTIFERA	Trichonis Lake	Amvrakia Lake	Lysimachia Lake	Ozeros Lake	Stratos Reservoir
Ascomorpha sp. (Perty, 1850)	+				
Asplanchna priodonta (Gosse, 1850)	+	+	+	+	+
Bdelloida	+	+			+
Brachionus angularis (Gosse, 1851)		+	+		
B. calyciflorus (Pallas, 1766)	+	+	+		+
B. c. f. anuraeiformis (Brehm, 1909)	+		+		
B. falcatus (Zacharias, 1898)			+		
Collotheca sp. (Harring, 1913	+	+	+		
Conochilus unicornis (Rousselet, 1892)	+	+	+	+	+
Euchlanis dilatata (Ehrenberg, 1832)	+				
Euchlanis sp.	+	+			
Epiphanes sp.			+		
Filinia longiseta (Ehrenberg, 1834)	+	+	+	+	+
F. opoliensis (Zacharias, 1898)	+		+	+	
F. terminalis (Plate, 1886)	+				
Gastropus stylifer (Imhof, 1891)	+		+		+
Hexarthra mira (Hudson, 1871)	+	+	+	+	+
H. intermedia (Wiszniewski, 1929)	+	+	+	+	
Kellicottia longispina (Kellicott, 1879)	+	+	+	+	
Keratella cochlearis (Gosse, 1851)	+	+	+	+	+
K. tecta (Gosse, 1851)		+	+	+	
K. tropica (Apstsein, 1907)		+	+	+	
K. quadrata (Müller, 1786)	+	+	+	+	

Table 2. (Continued)

ROTIFERA	Trichonis Lake	Amvrakia Lake	Lysimachia Lake	Ozeros Lake	Stratos Reservoir
Lecane luna (Müller, 1776)		+			
L. quadridentata (Ehrenberg, 1932)	+				+
Lecane sp.			+		
Monommata sp. (Bartsch, 1870)	+				
Notholca squamula (Müller, 1786)		+			
Ploesoma hudsoni (Imhof, 1891)	+	+	+	+	+
P. truncatum (Levander, 1894)	+				+
Polyarthra sp. (Ehrenberg, 1834)	+	+	+	+	+
Pompholyx sulcata (Hudson, 1885)	+	+	+		
Synchaeta sp. (Ehrenberg, 1832)	+	+	+	+	+
Trichocerca sp.		+	+	+	
T. capucina (Wierzejski, 1893)	+				
T. similis (Wierzejski, 1893)	+	+	+	+	+
Trichotria sp.			+		
COPEPODA					
Canthocamptus sp.					+
Eudiaptomus drieschi (Poppe & Mrazek, 1895)	+	+	+	+	+
Macrocyclops albidus (Jurine, 1820)	+	+	+	+	+
Microcyclops varicans (G.O. Sars, 1863)	+				+
Limnocalanus macrurus (G.O. Sars, 1863)					+
Thermocyclops dubowskii (Landé, 1890)		+			
CLADOCERA					
Alona sp. (Baird, 1843)	+	+			+
Bosmina longirostris (O.F.Muller, 1785)	+	+	+	+	+
Ceriodaphnia pulchella (Sars, 1862)	+	+	+	+	+

ROTIFERA	Trichonis Lake	Amvrakia Lake	Lysimachia Lake	Ozeros Lake	Stratos Reservoir
Daphnia cucullata (G.O. Sars, 1862)	+	+	+	+	+
D. galeata (Sars, 1864)	+				
D. longispina (O.F.M.)	+				
Diaphanosoma orghidani (Negrea, 1982)	+	+	+	+	+
Leptodora kindtii (Focke, 1844)	+		+	+	+
Moina micrura (Kurz, 1874)			+		
MOLLUSCA					
Dreissena blanci (Westerlund, 1890)	+	+	+	+	+

On the other hand, although the existence of several common species among the five lakes, nine species were unique and have been found only in a specific lake. Thus, the rotifers *Ascomorpha* sp. (Perty, 1850), *Euchlanis dilatata* (Ehrenberg, 1832), *Monommata* sp. (Bartsch, 1870), *Trichocerca capucina* (Wierzejski, 1893) and the cladocerans *Daphnia galeata* (Sars, 1864) and *D. longispina* (O.F.M.) were recorded only in Lake Trichonis. Similarly, the rotifer *Notholca squamula* (Müller, 1786) and the copepod *Thermocyclops dubowskii* (Landé, 1890) were found only in Lake Amvrakia, while *B. falcatus* (Zacharias, 1898), *Trichotria* sp. and the cladoceran *Moina micrura* (Kurz, 1874) were found only in Lysimachia Lake. Moreover, several species were present in only two, three or four lakes (Table 2), although the five lakes were situated in close distance (a few kilometers) among each other (Figure 1). There can be several explanations for these differences in the species composition among these aquatic ecosystems. First of all, although there was a consistent periodicity in the zooplankton survey and the sampling was usually performed in several locations within the lakes, there is a possibility of missing a number of species, especially these which were scarce in the water. This could be more complicated if the short life span of certain zooplankton groups like rotifers, is taken in mind. The variation in the morphometric elements, the specific characteristics, as well as the trophic conditions of the five lake ecosystems could have been also responsible for community differences. The lakes Trichonis and Amvrakia are large and deep ecosystems and are expected to contain larger numbers and also unique species, though the size of an aquatic ecosystem is not always accounted for its species richness. For instance, Lake Lysimachia is a small and shallow lake but proved to be very rich in zooplankton species, among which some unique for this ecosystem. The connection of this lake with Trichonis Lake and the constant water inflow from the latter could be responsible for the passive transportation of numerous species from Lake Trichonis to Lake Lysimachia. It should be noted here that communication between the two lakes is only one-way, meaning that water from Lysimachia does not enter Lake Trichonis and therefore it is unlikely that zooplankton species are actively transferred to the latter lake. The above suggests the importance of Lake Lysimachia from a biodiversity aspect, as well as the existence of certain ecological differences between lakes Trichonis and Lysimachia. Indeed, the former is an oligo- to mesotrophic lake while the latter is highly eutrophic (Chalkia and Kehayias, 2013a). It is well known that the trophicity of a lake can highly affect the structure of the zooplankton community (Gannon and Stemberger, 1978; Mäemets, 1983; Pejler, 1983) and there are several studies that have shown the usefulness of zooplankton species as indicators of alterations in the trophic dynamics and the ecological state of lakes (Jeppesen et al., 2011).

The particular hydrological characteristics of a lake can seriously affect the zooplankton community composition. Amvrakia Lake is a gypsum karst lake or sulphate lake, being rich in gypsum or calcium sulphate and having elevated conductivity values. Several studies found that the gypsum karst lakes are unique ecosystems that can even have different community composition compared to other nearby karstic lakes and, thus, they can represent some of the most interesting biotopes from the biodiversity point of view (Kuznetsova and Bayanov, 2001; Żurek, 2006; Stanković et al., 2010). Considering its faunistic composition, Lake Amvrakia showed certain differences with the other nearby lakes. Indeed, the rotifer *Notholca squamula* (Müller, 1786) and the copepod *Thermocyclops dybowskii* (Landé, 1890) were found only in this lake. On the other hand, the predator cladoceran *Leptodora kindtii* (Focke, 1884) was absent from this area although it is common to all the other lakes of western Greece. An explanation would involve the geological history of western Greece according to which Lake Amvrakia was part of a greater lake that had been created by the Acheloos River outflow at the end of the Pleiocene. Later on with the gradual diminishing of the water level, it was separated from the other karstic lakes of the area and continued as a completely independent aquatic ecosystem (Verginis and Leontaris, 1978), while the others are still connected by natural or man-made canals with the Acheloos River. Thus, it is possible that this long-lasting geographical isolation could have been responsible for the existence of different species of zooplankton in this basin. This has been also suggested by Spartinou (1992), who reported a great number of endemic species of algae in the phytoplankton of this lake.

The general similarities in species composition between the five aquatic ecosystems can be also attributed to their common origin. Moreover, as it was previously mentioned, some of them like Lake Lysimachia and Lake Trichonis are still connected, thus similarities in their species composition are to be expected. Furthermore, as the zooplankton community composition is concerned, the five lakes presented various similarities with other lakes of the western Greece, like Kalodiki Lake (Kagalou et al., 2010) and Pamvotis Lake (Antonopoulos et al., 2010), while less similarities with the lakes of the northern Greece such as Lake Mikri Prespa (Michaloudi et al., 1997), Lake Volvi (Zarfdjian et al., 1990), Lake Koroneia (Michaloudi and Kostecka, 2004). This could possibly be attributed to the geomorphological characteristics and evolution of the southern Balkans. Zogaris et al. (2009) using fish distributional patterns indicate that the Pindos Mountains create a prominent biogeographical discontinuity that separates distinct freshwater biogeographic "regions" west and east of Pindos. It is probable then, that the above mentioned lakes of western Greece, along with Lake Lysimachia, belong to the "Ionian" ecoregional unit (Zogaris et al., 2009), although this needs further verification.

TEMPORAL VARIATION

The total zooplankton abundance presented great variation among the five lakes and fluctuated from a minimum value of 2.56 ind l^{-1} in Lake Trichonis to the maximum density of 4449.3 ind l^{-1} in Lake Lysimachia. In particular, the minimum integrated average abundance in the 0-40 m in Lake Trichonis was recorded in January 2004 (2.56 ind l^{-1}), while the maximum value in March 2006 (73.9 ind l^{-1}). The respective minimum and maximum values in the 0-40 m water column in Lake Amvrakia were 57.2 and 348.7 ind l^{-1} (January and June 2007, respectively). In the other three lakes the zooplankton samples were collected within the 0-10 m depth and the minimum and maximum values were 147.9 and 4449.3 ind l^{-1} (February and May 2010, respectively) in Lake Lysimachia, 59.4 and 818.0 ind l^{-1} (February and April 2010, respectively) in Lake Ozeros, and 8.8 and 43.1 ind l^{-1} (February 2006 and July 2005) in Stratos Reservoir (Figure 2).

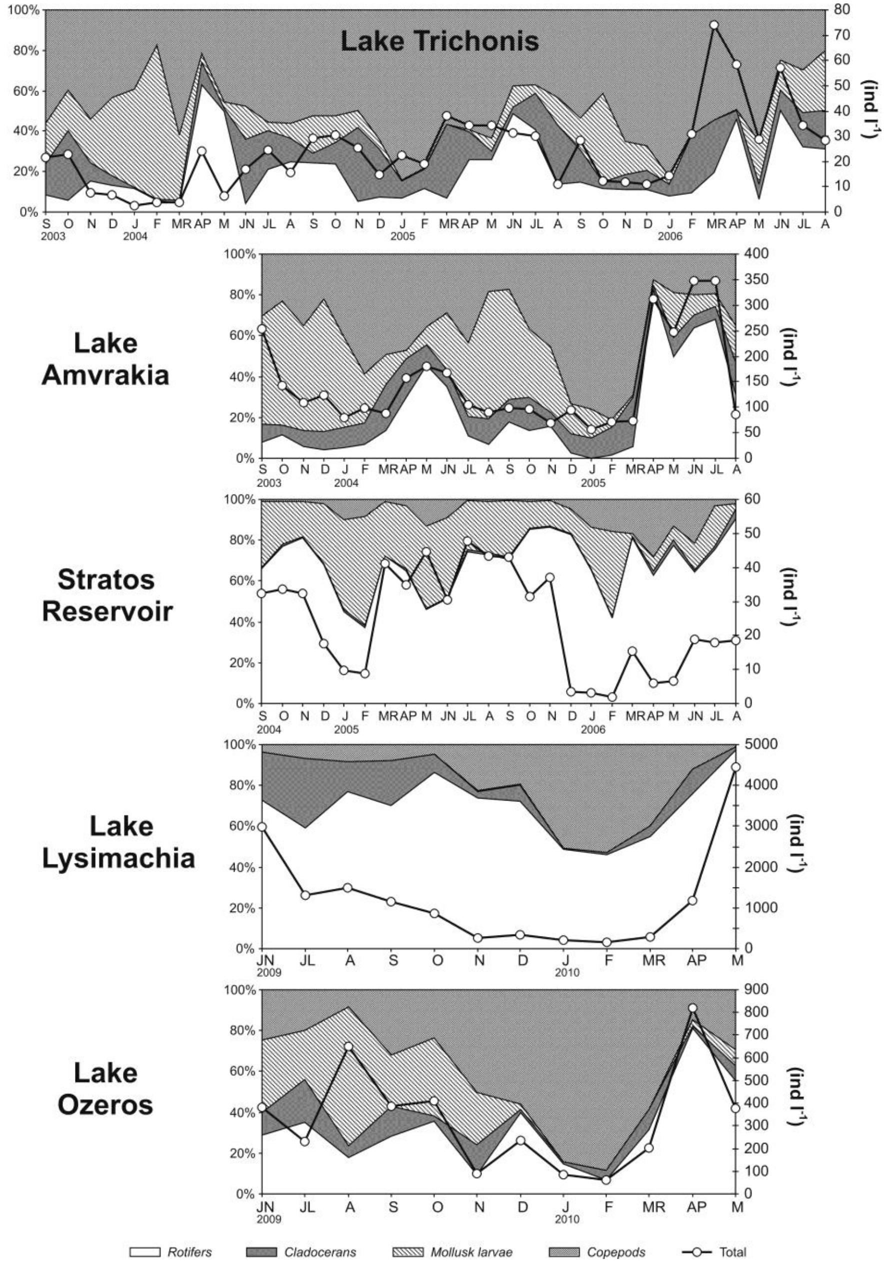


Figure 2. Monthly variation of the total zooplankton abundance (ind l^{-1}) and percentage (%) contribution of the main zooplanktonic groups in the five lakes studied.

The differences in the zooplankton density can be attributed to the different depths of the zooplankton sampling, e.g. usually the bulk of zooplankton concentrated at the surface 0-10 m layer of the deep lakes (Wetzel, 2001). Thus, valid comparisons can exist only between the two deep lakes (Trichonis and Amvrakia) and among the three shallow lakes (Lysimachia, Ozeros and Stratos Reservoir). The higher zooplankton abundance found in Lake Amvrakia in comparison to Lake Trichonis was probably ought to the greater trophicity of the former lake. Indeed, Lake Amvrakia is considered mesotrophic (Chalkia et al., 2012, Thomatou et al., 2013), whereas Lake Trichonis is an oligo- to mesotrophic lake (Doulka and Kehayias, 2008; Doulka 2010). Accordingly, Lake Lysimachia as highly eutrophic lake presented the highest zooplankton abundance and followed by Lake Ozeros, which is considered a meso-eutrophic ecosystem (Chalkia and Kehayias, 2013b) and Stratos Reservoir having oligo- to mesotrophic characteristics (Kehayias et al., 2008).

Copepods prevailed in the zooplankton community of the lakes Trichonis and Ozeros and accounted for 50.0 and 40.9 % respectively, while rotifers in Lake Lysimachia and in Stratos Reservoir (69.4 and 70.3 %, respectively). Lake Amvrakia characterized by the high average proportion of the larvae of *D. blanci* (37.3 %) during the first sampling year, while during the second year the mollusc larvae accounted for 14 % and the group of rotifers prevailed (48.2 %). The calanoid copepod *E. drieschi* was the dominant species among copepods in the four natural lakes and accounted for nearly 90 % (considering adults and copepodites) in most of them, except Lysimachia Lake (68.2 %). In contrast, this species accounted for 10.5 % in Stratos Reservoir, where the cyclopoid *M. albidus,* prevailed (88.9 %). The remaining cyclopoid copepods *Microcyclops varicans* (G.O. Sars, 1863) and *T. dybowskii* contributed a small proportion among copepods in all the lakes. The nauplii of copepods, which were not identified to species, accounted for a great proportion in the copepods community and they were found year-round in all lakes. The maximum abundance for *E. drieschi* was recorded in late winter to early spring in all lakes while the year-round presence of egg-bearing females of this species, as well as nauplii (most of which were *E. drieschi*), probably suggests that either it has multiple reproductive periods, or a continuous reproduction. On the other hand, the peak of abundance for *M. albidus* was recorded in late spring and especially in the summer months. In lakes Trichonis and Amvrakia the greater abundance values of this species usually coincided with the lowest values of *E. drieschi,* indicating probably competitive interaction between them (Doulka and Kehayias, 2008; Chalkia et al., 2012).

The highest abundance of rotifers in Lake Lysimachia was not a surprise considering that this group dominates the zooplankton community in eutrophic ecosystems (Wetzel, 2001). Also, although there was no estimation of the trophic condition of Stratos Reservoir (Kehayias et al., 2008), the dominance of rotifers in the zooplankton, along with the dominance of cyclopoid copepods in the crustacean community, and the presence of certain indicator species, suggest the eutrophic character of this ecosystem (McNaught, 1975; Geller and Müller, 1981; Pejler, 1983). Different species of rotifers prevailed in the five lakes, as the consequence of the variability in these ecosystems. Among the numerically most important rotifer species was *Kellicottia longispina* which was the dominant species in lakes Trichonis and Amvrakia, while it was present in low abundance in lakes Lysimachia and Ozeros, and it was absent from Stratos Reservoir. The species is considered indicator for oligotrophic conditions (Gannon and Stemberger, 1978; Mäemets, 1983; Pejler, 1983) which coresponds well to the trophic conditions of both lakes Trichonis and Amvrakia. *K. longispina* presented greater abundance in late spring to summer in all the lakes mentioned, having the highest average value in Lake Amvrakia (95.0 ind l^{-1}). *Conochilus unicornis* dominated the rotifers community in Ozeros Lake and it was among the most abundant species in lakes Trichonis, Amvrakia and Lysimachia. There was almost similar seasonal variation of this species in all the above lakes, with the peak of its abundance being recorded in April and May (Tables 3-7). *Keratella cochlearis* is among the most common species in the European freshwater ecosystems and it was present in all the lakes in study, where dominated the rotifers community in Stratos Reservoir and in Lake Lysimachia. The species is considered indicator of eutrophic conditions (Gannon and Stemberger, 1978; Mäemets, 1983; Pejler, 1983) and this was probably the explanation of its lowest density in Lake Trichonis in comparison to the other lakes of the area. The species was present year-round in most of the lakes and presented increased abundance in the period from April to September (Tables 3-7). Individuals belong to the genus *Polyarthra* sp. were common in all the lakes with higher density in Lake Amvrakia (Table 4). *Polyarthra* sp. were third in abundance in Stratos Reservoir and the lakes Lysimachia and Ozeros, where presented higher values from April to October. *Gastropus stylifer* (Imhof, 1891) was second in abundance among rotifers in Lake Trichonis (Table 3), it was also abundant in Stratos Reservoir and in Lake Lysimachia, but it was not found in lakes Amvrakia and Ozeros.

Table 3. Monthly average abundance (ind l^{-1}) variation of the ten numerically most important rotifer species, the species of copepods, cladocerans and the larvae of *Dreissena blanci* found during September 2003 to August 2006 in Lake Trichonis. The average % percentage of each species contribution to the zooplankton community is also given.

ROTIFERA	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	(%)
Asplanchna priodonta	0.41	0.25	0.00	0.00	0.00	0.01	0.00	0.06	0.18	0.01	0.00	0.50	0.5
Conochilus unicornis	0.01	0.01	0.00	0.00	0.00	0.04	1.68	3.91	0.00	1.60	0.67	0.38	2.9
Filinia longiseta	0.17	0.12	0.00	0.02	0.04	0.02	0.16	1.31	0.13	0.79	0.21	0.41	1.2
Gastropus stylifer	1.62	1.58	0.04	0.01	0.01	0.01	0.00	5.60	2.43	2.08	1.48	0.19	5.2
Hexarthra mira	0.31	0.39	0.08	0.14	0.10	0.36	0.26	0.21	0.00	0.01	0.03	0.05	0.7
Kellicottia longispina	0.51	0.31	0.37	0.50	0.52	0.79	1.86	2.30	1.26	7.60	3.88	1.46	7.4
Ploesoma truncatum	0.38	0.21	0.00	0.00	0.00	0.00	0.00	0.17	0.00	0.55	0.66	0.49	0.9
Pompholyx sulcata	0.12	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.04	1.41	0.64	0.16	0.8
Synchaeta sp.	0.37	0.06	0.00	0.00	0.00	0.06	0.00	0.02	0.01	0.29	1.10	0.51	0.8
Trichocerca similis	0.07	0.09	0.02	0.14	0.17	0.18	1.34	2.33	0.03	0.01	0.08	0.04	1.6
COPEPODA													
Eudiaptomus drieschi	7.84	6.79	6.25	4.39	6.25	5.11	12.92	9.84	10.72	7.59	7.74	3.68	30.9
Macrocyclops albidus	0.04	0.15	0.21	0.25	0.09	0.08	0.14	0.35	0.30	0.03	0.02	0.02	0.6
Microcyclops varicans	0.06	0.01	0.11	0.04	0.00	0.06	0.04	0.00	0.00	0.00	0.00	0.00	0.1
Nauplii	6.29	3.10	1.48	1.85	4.22	6.33	8.24	7.96	3.33	3.72	3.86	2.75	18.4
CLADOCERA													
Alona sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.0
Bosmina longirostris	0.44	0.80	0.83	1.25	0.14	0.84	1.88	1.73	0.04	1.10	2.24	0.22	4.0
Ceriodaphnia pulchella	0.00	0.00	0.00	0.00	0.00	0.17	0.30	0.08	0.00	0.01	0.01	0.00	0.2
Daphnia cucullata	0.02	0.04	0.05	0.04	0.12	1.66	4.57	1.04	0.90	0.66	0.07	0.00	3.2
Daphnia galeata	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.25	0.06	0.01	0.01	0.00	0.1
Diaphanosoma orghidani	2.63	3.02	2.70	0.34	0.63	0.57	4.27	0.13	0.20	2.20	2.97	3.22	7.9
Leptodora kindtii	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.0
MOLLUSCA													
Dreissena blanci	4.77	4.67	1.91	1.53	0.67	1.00	0.40	0.54	2.80	4.84	3.17	3.68	10.4

Table 4. Monthly average abundance (ind l^{-1}) variation of the ten numerically most important rotifer species, the species of copepods, cladocerans and the larvae of *Dreissena blanci* found during September 2006 to August 2008 in Lake Amvrakia. The average % percentage of each species contribution to the zooplankton community is also given.

ROTIFERA	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	(%)
Asplanchna priodonta	0.14	0.21	4.10	0.28	0.59	1.27	0.01	0.85	0.64	4.46	0.27	0.48	0.8
Collotheca sp.	8.50	7.33	1.66	0.00	0.00	0.85	0.38	0.11	0.18	0.44	0.85	1.39	1.2
Conochilus unicornis	0.52	0.00	0.12	0.79	0.17	0.38	4.87	144.31	31.44	7.25	0.20	0.25	10.9
Filinia longiseta	1.40	0.39	0.09	0.03	0.01	0.10	0.37	1.56	5.01	16.89	12.34	0.56	2.2
Hexarthra intermedia	0.01	0.06	0.00	0.07	0.00	0.00	0.00	0.00	0.42	1.88	11.00	0.00	0.8
Kellicottia longispina	2.90	4.73	1.49	2.24	0.74	0.87	2.47	5.25	20.60	85.01	95.03	12.82	13.4
Keratella cochlearis	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.06	3.21	12.83	2.01	0.00	1.0
Keratella quadrata	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.06	4.35	0.42	0.01	0.00	0.3
Polyarthra sp.	1.81	1.27	0.31	0.00	0.00	0.00	0.00	0.00	5.99	5.31	0.26	0.08	0.9
Pompholyx sulcata	1.57	0.18	0.27	0.04	0.01	0.00	0.00	0.04	30.33	5.86	1.76	0.43	2.3
COPEPODA													33.8
Eudiaptomus drieschi	28.15	14.46	12.60	14.89	23.66	32.09	30.33	33.53	23.82	29.51	24.68	10.71	15.9
Macrocyclops albidus	1.54	1.28	0.56	1.74	1.01	1.29	1.03	2.53	6.82	6.73	3.98	0.96	1.7
Thermocyclops dybowskii	0.76	1.28	1.37	1.12	0.49	1.34	1.00	1.02	0.56	0.50	0.13	0.84	0.6
Nauplii	16.31	17.25	20.09	30.44	12.79	22.73	14.50	19.06	24.12	22.31	27.98	10.75	13.7
CLADOCERA													31.9
Alona sp.	0.00	0.41	0.06	0.48	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.1
Bosmina longirostris	1.19	2.49	2.05	3.73	0.48	5.16	8.23	8.56	13.00	5.63	2.00	3.77	3.2
Ceriodaphnia pulchella	5.37	1.95	1.85	5.21	2.36	0.47	1.05	0.50	0.75	4.28	6.30	3.15	1.9
Daphnia cucullata	0.60	0.36	0.21	0.66	1.22	2.70	7.76	7.51	3.08	2.05	1.42	0.57	1.6
Diaphanosoma orghidani	10.10	7.73	2.73	3.66	2.85	1.67	1.56	1.31	3.91	5.59	6.41	5.10	3.0
MOLLUSCA													9.8
Dreissena blanci	93.77	60.09	38.95	47.26	21.66	13.14	6.95	7.42	34.93	40.15	29.24	35.87	24.6

Table 5. Monthly average abundance (ind l^{-1}) variation of the ten numerically most important rotifer species, the species of copepods, cladocerans and the larvae of *Dreissena blanci* found during September 2004 to August 2006 in Stratos Reservoir. The average % percentage of each species contribution to the zooplankton community is also given.

ROTIFERA	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	(%)
Asplanchna priodonta	0.06	0.20	0.13	0.12	0.01	0.05	1.52	0.50	0.23	0.36	0.11	0.70	1.4
Brachionus calyciflorus	0.00	0.00	0.01	0.00	0.54	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.2
Bdelloida	0.81	1.82	2.55	1.22	1.42	1.48	13.05	4.17	0.78	1.88	0.52	2.45	11.1
Gastropus stylifer	2.67	3.91	3.55	0.69	0.11	0.03	0.00	0.02	1.52	0.96	2.35	1.03	5.8
Keratella cochlearis	18.30	17.54	19.63	4.15	0.56	0.13	0.07	4.12	0.94	3.86	8.24	11.47	30.7
Lecane quadridenticata	0.00	0.02	0.07	0.07	0.01	0.00	0.00	0.04	0.02	0.04	0.00	0.04	0.1
Ploesoma hudsoni	0.06	0.05	0.06	0.03	0.00	0.00	0.02	0.01	0.06	0.02	4.40	1.37	2.1
P. truncatum	1.60	0.03	0.04	0.01	0.00	0.00	0.00	0.02	0.03	0.03	8.31	3.93	4.8
Polyarthra sp.	2.16	2.39	2.66	0.96	0.49	0.16	1.82	1.29	8.55	5.60	0.42	2.90	10.1
Synchaeta sp.	0.22	0.29	0.31	0.12	0.11	0.19	4.65	3.09	0.72	1.01	0.09	0.19	3.8
COPEPODA													
Eudiaptomus drieschi	0.00	0.01	0.01	0.01	0.05	0.01	0.02	0.04	0.09	0.08	0.09	0.00	0.1
Macrocyclops albidus	0.03	0.05	0.05	0.06	0.31	0.09	0.34	0.45	0.71	1.34	0.03	0.02	1.2
Microcyclops varicans	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.0
Canthocamptus sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.0
Limnocalanus macrurus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.0
Nauplii	0.22	0.21	0.19	0.19	0.34	0.40	1.10	0.94	2.61	1.91	0.31	0.37	3.0
CLADOCERA													
Alona sp.	0.00	0.00	0.01	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.0
Bosmina longirostris	0.13	0.16	0.10	0.02	0.02	0.02	0.04	0.15	0.10	0.09	0.23	0.32	0.5
Ceriodaphnia pulchella	0.02	0.02	0.03	0.01	0.01	0.00	0.00	0.00	0.00	0.02	0.03	0.05	0.1
Daphnia cucullata	0.11	0.06	0.04	0.01	0.01	0.01	0.02	0.04	0.03	0.06	0.09	0.15	0.2
Diaphanosoma orghidani	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.01	0.02	0.0
Leptodora kindtii	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.0
MOLLUSCA													
Dreissena blanci	11.28	5.65	5.16	2.76	2.44	2.76	5.64	5.66	9.23	7.25	7.53	5.68	24.5

Table 6. Monthly average abundance (ind l^{-1}) variation of the ten numerically most important rotifer species, the species of copepods, cladocerans and the larvae of *Dreissena blanci* found during June 2009 to May 2010 in Lake Lysimachia. The average % percentage of each species contribution to the zooplankton community is also given.

ROTIFERA	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	AVG	(%)
Asplanchna priodonta	77.45	10.84	36.69	28.54	49.59	95.80	2.04	1.35	1.02	3.38	0.67	21.69	27.42	3.9
Conochilus unicornis	0.00	33.96	29.88	4.08	0.00	2.04	0.00	24.46	9.51	4.75	50.26	233.66	32.72	4.6
Filinia opoliensis	695.68	334.27	168.48	27.15	68.61	20.38	2.71	0.00	0.00	0.00	0.00	2.69	110.00	15.5
Gastropus stylifer	0.00	0.00	0.00	0.00	0.00	2.71	0.34	1.35	0.67	0.00	6.11	274.43	23.80	3.4
Hexarthra mira	97.83	58.42	171.21	29.88	12.90	0.00	0.00	0.00	0.00	0.67	0.00	2.69	31.13	4.4
Keratella cochlearis	40.76	24.46	520.40	73.38	8.83	4.08	41.10	6.11	13.92	6.11	122.97	578.85	120.08	16.9
Keratella tropica	197.01	13.57	42.11	1.35	14.94	0.00	0.00	0.00	1.02	0.00	0.00	0.00	22.50	3.2
Polyarthra sp.	52.99	21.73	160.33	71.99	68.61	19.02	23.09	62.49	3.73	8.83	97.14	73.38	55.28	7.8
Synchaeta sp.	180.71	9.50	0.00	23.07	78.12	6.79	6.45	16.31	7.81	57.07	23.09	21.69	35.88	5.1
Trichocerca similis	122.29	14.92	20.38	1.35	0.67	0.00	0.00	0.00	0.00	0.00	0.00	5.38	13.75	1.9
COPEPODA														
Eudiaptomus drieschi	48.92	29.84	4.04	8.11	13.55	14.25	15.61	46.84	13.92	42.09	30.55	36.67	25.37	3.57
Macrocyclops albidus	1.35	16.26	77.37	39.38	3.38	1.35	0.34	0.67	0.67	0.00	0.67	0.67	11.84	1.67
Nauplii	84.22	36.69	84.22	52.99	34.65	55.03	47.55	40.76	31.59	34.65	47.55	7.46	46.45	6.54
CLADOCERA														
Moina micrura	40.76	5.42	1.35	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.96	0.6
Bosmina longirostris	392.68	301.66	240.51	127.71	33.28	0.67	7.47	0.67	1.69	13.57	17.65	50.96	99.04	13.9

ROTIFERA	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	AVG	(%)
Ceriodaphnia pulchella	0.00	1.35	10.84	2.69	0.00	0.00	0.00	0.00	0.00	0.67	4.08	2.04	1.81	0.3
Daphnia cucullata	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.67	12.90	2.04	1.30	0.2
Diaphanosoma orghidani	78.80	54.34	42.11	76.07	40.07	4.75	0.00	0.00	0.00	0.00	2.04	27.84	27.17	3.8
Leptodora kindtii	0.13	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.0
MOLLUSCA														
Dreissena blanci	0.00	0.00	0.00	0.00	0.00	0.00	3.39	0.00	0.00	0.00	0.00	0.00	0.28	0.0

Table 7. Monthly average abundance (ind l^{-1}) variation of the ten numerically most important rotifer species, the species of copepods, cladocerans and the larvae of *Dreissena blanci* found during June 2009 to May 2010 in Lake Ozeros. The average % percentage of each species contribution to the zooplankton community is also given.

ROTIFERA	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	(%)
Asplanchna priodonta	0,00	0,00	0,00	0,00	16,97	5,52	0,00	0,00	0,21	0,00	5,94	21,22	1,3
Conochilus unicornis	0,00	0,00	0,00	0,00	0,00	0,00	90,85	0,00	0,21	0,00	242,04	212,31	13,7
Filinia longiseta	43,31	3,39	11,03	5,10	11,03	0,84	11,03	5,10	2,12	0,42	13,58	28,03	3,4
Hexarthra sp.	0,00	46,70	70,47	7,64	0,84	0,00	0,00	0,00	0,00	0,00	0,00	2,55	3,2
Keratella cochlearis	0,00	2,55	1,68	0,00	1,68	0,84	3,39	0,00	0,00	0,00	0,84	13,58	0,6
Keratella tropica	1,68	0,00	3,39	0,00	0,00	0,42	0,84	0,00	0,85	0,00	0,00	0,00	0,2
Keratella quadrata	0,00	0,00	0,84	0,00	0,00	0,00	1,68	2,11	1,48	42,46	1,68	0,00	1,3
Polyarthra sp.	1,68	10,19	9,32	76,43	95,11	3,82	0,84	0,00	0,00	0,00	0,84	2,55	5,1
Synchaeta sp.	36,51	15,29	42,45	9,32	73,02	1,27	0,00	0,00	0,00	0,00	181,73	22,06	9,6
Trichocerca similis	0,84	5,10	6,78	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,3
COPEPODA													
Eudiaptomus drieschi	55,35	19,26	28,85	38,19	51,11	32,89	40,43	30,26	20,92	57,65	74,57	34,98	12,2
Macrocyclops albidus	0,48	0,84	0,84	0,42	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,1
Nauplii	39,23	26,55	26,08	84,37	46,09	13,16	91,22	39,85	31,59	60,84	46,95	75,82	14,6
CLADOCERA													
Bosmina longirostris	2,11	1,69	0,48	0,48	0,90	0,24	1,80	0,64	1,86	0,21	6,90	6,42	0,6
Ceriodaphnia pulchella	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,66	0,0
Daphnia cucullata	0,42	0,00	0,00	0,00	0,00	0,00	0,00	0,33	1,01	18,71	2,34	0,90	0,6
Diaphanosoma orghidani	38,93	47,61	34,69	55,38	9,33	13,34	1,69	0,00	0,00	0,48	2,34	18,93	5,6
Leptodora kindtii	0,03	0,00	0,09	0,08	0,03	0,03	0,00	0,00	0,02	0,00	0,09	0,01	0,0
MOLLUSCA													
Dreissena blanci	136,24	53,91	440,27	97,41	158,02	23,56	6,42	0,00	0,00	0,00	22,08	29,90	24,4

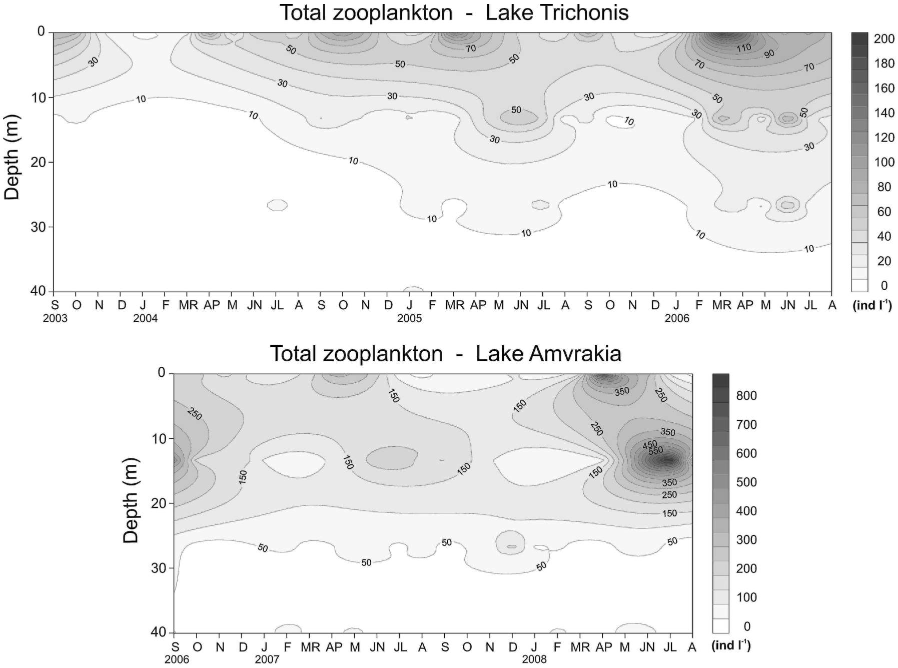
The seasonal maxima of this species were recorded in April-May (Trichonis, Lysimachia), but also in autumn (Stratos Reservoir). Finally, *Filinia longiseta* was found in all lakes being more abundant in Lake Lysimachia and in Lake Ozeros from May to July.

Cladocerans were numerically less important in the zooplankton community of all lakes and accounted for average proportions between 0.8 % in Stratos Reservoir to 18.8 % in Lake Lysimachia. *Bosmina longirostris* and *Diaphanosoma orghidani* were the most important cladoceran species in all cases. *B. longirostris* was the dominant species among cladocerans in lakes Amvrakia, Lysimachia and in Stratos Reservoir, while *D. orghidani* in lakes Trichonis and Ozeros (Tables 3-7). A seasonal succession between *B. longirostris* which prevailed in the colder periods and *D. orghidani* which prevailed in the warmer ones was recorded in lakes Trichonis, Amvrakia and Ozeros. This phenomenon could be owed to the different food preferences of these species. Thus, *D. orghidani* as a highly efficient bacteriofeeder was present in summer, while *B. longirostris* as a low efficient bacteriofeeder was present mainly in late winter to spring (Geller and Müller, 1981). Moreover, seasonal succession were found between *D. orghidani* and *Daphnia cucullata* in lakes Trichonis and Amvrakia, similar to the pattern reported by Michaloudi et al. (1997) in Lake Mikri Prespa, and could be ought to competitive interactions between these species (Matveev 1987). *D. cucullata* was found in all lakes showing higher density values in lakes Lysimachia and Ozeros, while showed pick of abundance in March and April. This species is abundant in eutrophic lakes of Europe (Gannon and Stemberger, 1978; Gliwicz and Lampert, 1990) and considered as indicator species for that type of ecosystems. This probably explains its higher abundance in lakes Lysimachia and Ozeros, which are having higher trophicity in comparison to the other lakes. *Moina micrura* is commonly regarded as a cosmopolitan cladoceran species which can be found in all types of limnetic habitats, almost all over the world except for arctic and cold-temperate regions (Petrusek et al., 2004). In the present investigation *M. micrura* was found only in Lake Lysimachia and, although it had been recorded at the early ‘50s in lakes of the northern Greece (e.g. Koroneia) and in ponds of the Corfu Island (Zarfdjian and Economidis, 1989), it is the first record of this species in the southern Greece and can be considered as the first recent record in the country (Chalkia and Kehayias, 2013a). *M. micrura* was present in higher abundance in June. Finally, the predator cladoceran species *Leptodora kindtii* was found mainly from late spring to summer in lakes Trichonis, Lysimachia and Ozeros, while it was absent from Lake Amvrakia and Stratos Reservoir.

Dreissena blanci larvae were almost constantly found in the zooplankton samples from the five lakes, though there were certain differences in their abundance among them. The highest density values were recorded in Lake Ozeros reaching up to 440.0 ind l^{-1} in August 2010 (Table 7). On the other hand, the larvae were nearly absent from the zooplankton in Lake Lysimachia, where only a few specimens were found in a single sampling occasion. Several studies have shown that mud and sand are unsuitable substrates for the settlement of the larvae of the sister species *Dreissena polymorpha* (see in Lewandowski 1982). Thus, considering that Lake Lysimachia has muddy bottom substratum, which is in contrast to the rocky structure of the bottom of the other lakes, it is reasonable to assume that this was the restricting factor for the presence of *D. blanci* larvae in this area (Kehayias et al., 2012). Differences in the abundance of the *D. blanci* larvae were found between two consecutive years of study in Stratos Reservoir and in Lake Amvrakia (Figure 2). Indeed, in Stratos Reservoir the larvae presented higher abundance during the first year of study (September 2004-August 2005) in comparison to the second one (September 2005-August 2006), which was attributed to the greater water outflow in the area during the latter period (Kehayias et al., 2012). Furthermore, the drop of the water level in Lake Amvrakia during the second sampling period (September 2007-August 2008) was probably responsible for the decrease in the abundance of the larvae of this species in this period. The explanation suggested by Kehayias et al (2012) was that the drop of water level in the second period, uncovered an extended area of the bottom of the lake, which was the habitat for the adult forms of this mollusk and, thus, resulted to the diminishing of the overall reproductive capacity of the population.

VERTICAL DISTRIBUTION

The investigation of the vertical distribution patterns of the zooplankton was performed in the two deep lakes Trichonis and Amvrakia in the period September 2003-August 2006 and September 2006-August 2008, respectively. Both lakes share common hydrological features and exhibit a long period of thermal stratification which starts in April and lasts till November (Doulka, 2010; Chalkia, 2013). The total zooplankton in both lakes presented a distributional pattern according to which the majority of the specimens tend to concentrate within the surface 0-10 or 0-20 m, while the deepest layers close to the bottom are the less populated (Figure 3). This pattern is common in deep stratified lakes and is enhanced by the water stratification (Hanazato, 1992; Wetzel, 2001).



Total zooplankton - Lake Trichonis

Total zooplankton - Lake Amvrakia

Figure 3. Monthly vertical profiles of the total zooplankton abundance (ind l^{-1}) in the deeper water station of lakes Trichonis and Amvrakia.

Indeed, in the periods when the thermocline (metalimnion) was strong the zooplankton was concentrated in the epilimnion in Lake Trichonis, while in Lake Amvrakia the median depth of the total community was recorded in greater depths. In winter, though, the vertical distribution of the zooplankton was uniform as the result of the water turnover in both lakes. This seasonal trend was constant through the sampling years with no statistically significant differences among these periods for each lake (Kruskal-Wallis test, $p>0.05$). However, although the existence of similarities between the two lakes, the total zooplankton in Lake Amvrakia presented deeper distribution than in Lake Trichonis throughout the sampling months when the median depths were taken into consideration (U-test, $p<0.05$).

Copepods in Lake Trichonis were more abundant within the upper 0-10 m, while in Lake Amvrakia they showed a tendency to concentrate close or within the boundaries of the metalimnion especially during the period of intense stratification e.g. June to October (Figure 4). *Eudiaptomus drieschi*, as the dominant species in both lakes, was responsible for the above trend. *Macrocyclops albidus*, instead, showed deeper distribution than *E. drieschi*, although there were no statistically significant differences in their median depths in any of the lakes (U-test, $p>0.05$). The adults and copepodites of the copepod *E. drieschi*, as well as the copepod nauplii, had similar vertical distribution throughout the sampling period in Lakes Trichonis (Kruskal-Wallis test, $p>0.05$), but not in Lake Amvrakia where nauplii distributed deeper than the adults and copepodites (Kruskal-Wallis test, $p<0.05$). The deeper distribution of nauplii in comparison to the older ontogenetic stages of copepods could be related to the reduction of food competition (Zadereev and Tolomeyev, 2007; Rejas et al., 2007), while the selection of the deeper layers by nauplii could be the result of their lower tolerance to the ultraviolet radiation (Leech and Williamson, 2000).

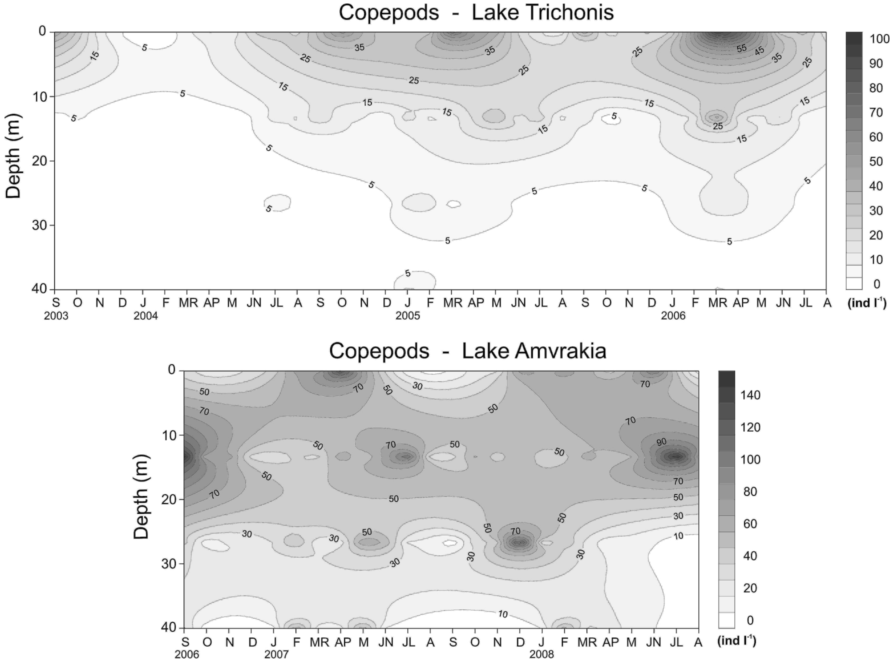


Figure 4. Monthly vertical profiles of the abundance (ind l^{-1}) of the copepod's community in the deeper water station of lakes Trichonis and Amvrakia.

Comparison of the vertical distribution of *E. drieschi*, as well as the total copepod community, between the two lakes using their median depths revealed statistically significant difference (U-test, $p<0.05$), with deeper distribution in Lake Amvrakia. In contrast, no differences between the two lakes were obtained in the vertical distribution of *M. albidus* (U-test, $p>0.05$). *Thermocyclops dybowskii* in Lake Amvrakia had considerably deeper distribution than *E. drieschi* and *M. albidus* (U-test, $p<0.05$), with its median depths being generally deeper than 20 m. Moreover, a considerable number of *T. dybowskii* specimens were found even in the deepest layers of 35 to 40 m, where probably could be benefited by the presence of dead organic matter (Papinska, 1985; Caramujo and Boavida, 2000).

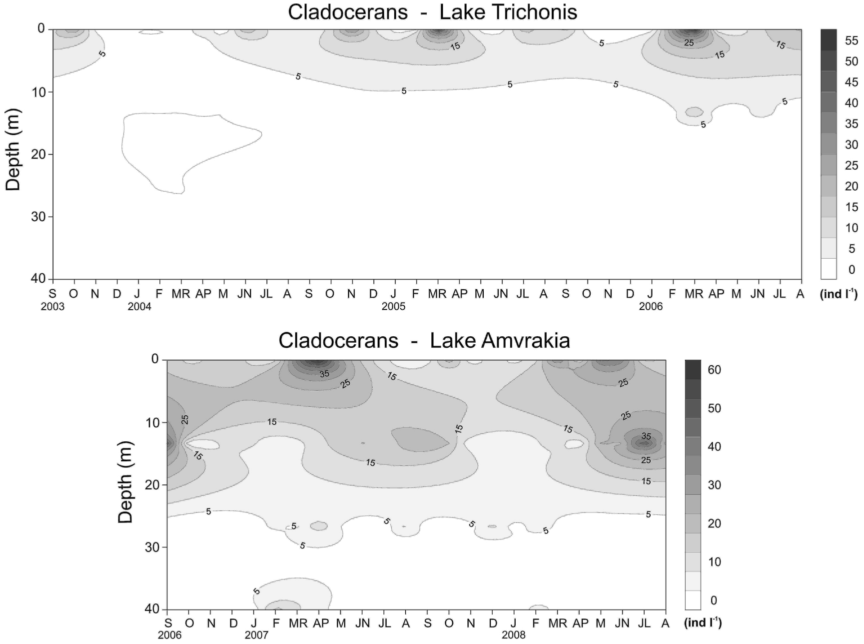


Figure 5. Monthly vertical profiles of the abundance (ind l^{-1}) of the cladoceran's community in the deeper water station of lakes Trichonis and Amvrakia.

Cladocerans presented the shallowest distribution among the other zooplankton groups in both lakes, with the bulk of specimens concentrated in the upper 0-10 m in Lake Trichonis, or 0-20 m in Lake Amvrakia during the stratification period, while having a more uniform distribution in the winter (Figure 5). There was also significant difference between the two lakes in the median depths of total cladocerans (U-test, $p<0.05$), as well as of the species being common in them, like *Bosmina longirostris* and *Diaphanosoma orghidani* (U-test, $p<0.05$), while no differences were found for the vertical distribution of *Daphnia cucullata* (U-test, p>0.05). In both lakes, there was a vertical separation of the most important cladoceran species with *D. orghidani* and *D. cucullata* occupied shallower depths than *Bosmina longirostris* in most cases, although this was not statistically verified in Lake Trichonis. Considering the seasonal and vertical distribution of the above three cladoceran species it is noteworthy that when there was concurrence in the vertical distributions of species only one of them prevailed, while if the species had equal abundances, there was a vertical separation. Thus, it could be suggested that cladocerans seem to have adopted certain ecological strategies, such as space- or time-separation in order to reduce inter-specific competition, since competitive interactions have been reported for *Bosmina*, *Daphnia* and *Diaphanosoma* species (DeMott and Kerfoot, 1982; Matveev, 1987). However, more complex interactions could be established in lake ecosystems since competition can be seen also among copepods and cladocerans (McNaught 1975; Muck and Lampert, 1984).

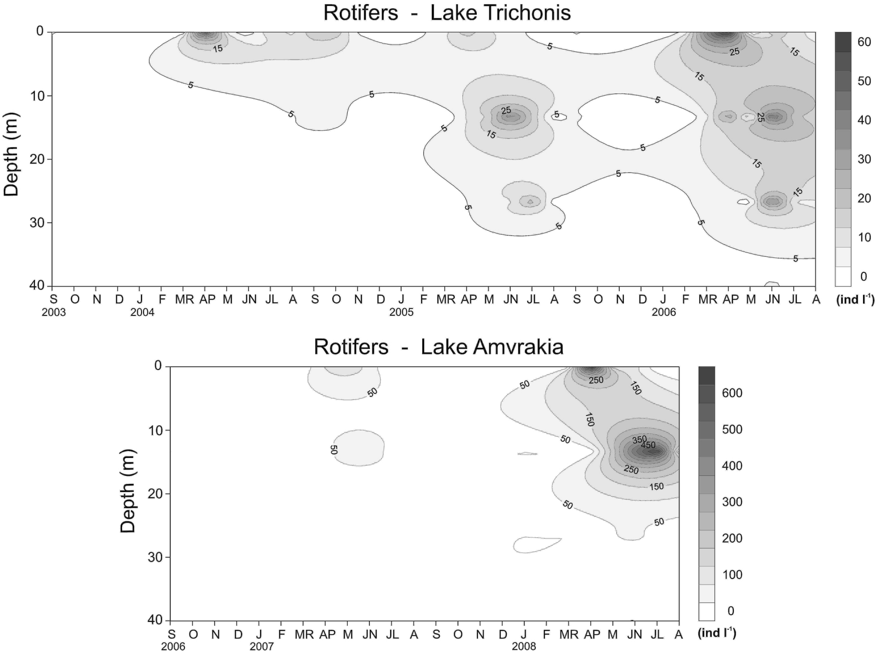


Figure 6. Monthly vertical profiles of the abundance (ind l^{-1}) of the rotifer's community in the deeper water station of lakes Trichonis and Amvrakia.

The total rotifer's community presented a variable vertical distribution which was affected by the dominance of certain species in different periods (Figure 6). Considering the median depths of rotifers in both lakes, a distinct vertical separation of species was recorded. Statistically significant differences were recorded between the median depths of the numerically most important species *K. longispina*, *G. stylifer* and *Ploesoma* sp. in Lake Trichonis, with *K. longispina* having the deepest distribution and *Ploesoma* sp. the shallowest (Kruskal-Wallis test, $p<0.05$). In the same area, vertical separation was also found for the other three important rotifer species, *Brachionus calyciflorus*, *Hexarthra* sp. and *Synchaeta* sp., with the former being deeper than the others and the latter having the shallowest distribution. The same phenomenon was also recorded in Lake Amvrakia among the most abundant species *Conochilus unicornis*, *Filinia longiseta* and *K. longispina* for the periods in which the three species coexisted. In this case, *F. longiseta* was found to distribute deeper, while *C. unicornis* was having the shallower vertical position. On the other hand, there were no differences between lakes Trichonis and Amvrakia considering the vertical distribution of all the rotifer species being common in them.

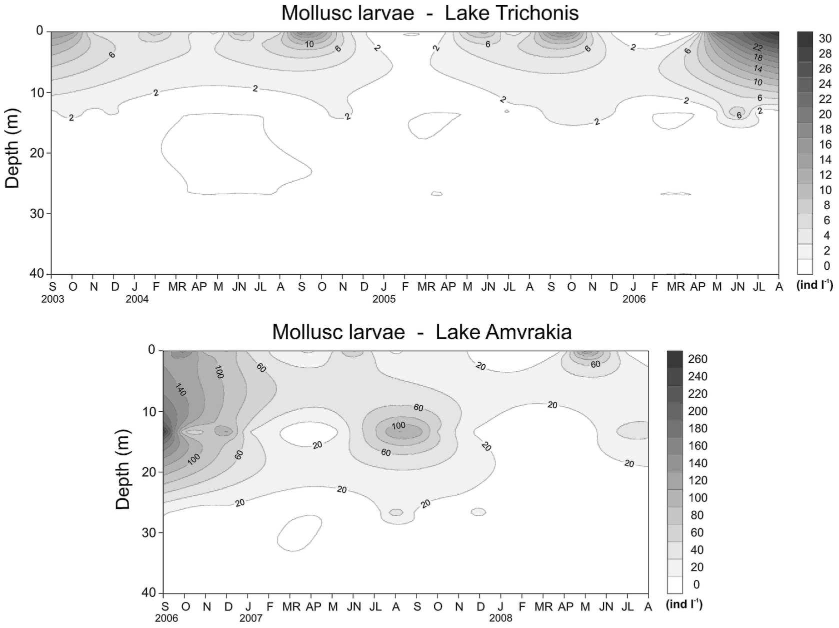


Figure 7. Monthly vertical profiles of the abundance (ind l^{-1}) of the *Dreissena blanci* larvae in the deeper water station of lakes Trichonis and Amvrakia.

Finally, the greater proportion of the abundance of *Dreissena blanci* larvae was recorded in the upper 20 m in both lakes (Figure 7) and was diminishing with depth, especially during the stratification period (May to October). Several studies on the vertical distribution of the relative species *D. polymorpha*, reported maxima of abundance in the upper 10 m, or within the epilimnion (Sprung, 1993). The vertical distributions of the *D. blanci* larvae differed significantly between the two lakes considering their median depths (U-test, $p<0.015$), with the larvae having deeper distribution in Lake Amvrakia. In the latter, during the stratification period, the larvae aggregated above or close to the thermocline layer, while their vertical distribution in the overturn period (November to April) was rather uniform (Figure 7). It is worth to note that, although the general diminishing of abundance with increasing depth in Lake Amvrakia, specimens of *D. blanci* larvae were also present in the hypoxic (and sometimes anoxic) deeper layers near to the bottom.

In conclusion, it is remarkable that most of the zooplankton species and groups maintained the same pattern of vertical distribution in both sampling years, so as no significant differences were recorded between them. This stability in the vertical distribution probably means that the species in the two lakes have adapted a vertical position which proved beneficial for their survival. Thermal stratification in both lakes Trichonis and Amvrakia played a critical role on the vertical distribution of the zooplankton groups. In deep lakes with thermal stratification a pattern of vertical separation of species is common (Hanazato, 1992; Armengol-Diaz et al., 1993) and is enhanced by interspecific competition, especially in cases of low food availability (Wetzel, 2001). However, the explanations of this phenomenon implies several ecological elements, such as the variation of the physicochemical parameters, the vertical distribution of phytoplankton and bacterioplankton as the major source of energy for the pelagic zooplankton, the predation pressure exercised by fish species, and also the species specific ethological behavior. The explanation for the differences in the vertical distribution of several species and groups between lakes Trichonis and Amvrakia is rather difficult considering their hydrological similarities and their proximity. It is possible that the deeper distribution of zooplankton in Lake Amvrakia was ought to differences in the abundance, the composition and the vertical distribution of the phytoplankton community, though, the verification of this hypothesis would require data on the above biotic elements.

INTERRELATION WITH ABIOTIC ELEMENTS

There are numerous studies pointing out the importance of physical and chemical parameters on the community structure and the zooplankton dynamics in lakes. In the present study we selected to present the results of this interrelation for the three out of five lakes, for which there has been at least a two-year study, to increase the total number of observations and thus, the accuracy of the methodology used. The results of the CCA analysis in Lake Trichonis showed that the first two axes used in the ordination diagram (Figure 8) explain 45.5 % of the total variability in the species data (32.0 % and 13.5 % for axis 1 and 2, respectively). Among the examined environmental variables, the longest arrows represent temperature, chl-a and DO concentration, meaning that these are strongly correlated with the ordination axes (axis 1: DO, NO_2, NO_3 and axis 2: temperature and chl-a) and more closely related to the pattern of species variation shown in the diagram (Figure 8). Temperature was the most important parameter and explained almost 80 % of the species seasonal variability. The concentration of chl-a and DO were second and third in significance and explained 55 % and about 39 % of the variability (Table 8). Temperature was the most important factor for the variation of *Keratella cochlearis* as well as for *Hexarthra intermedia*, the larvae of *Dreissena blanci* and *Diaphanosoma orghidani* (Figure 8). Among the other species *Conochilus unicornis* was mostly affected by chl-a and DO, while the remaining species were less affected by a specific parameter.

In Lake Amvrakia the first two axes used in the ordination diagram (Figure 8) explain 80.5 % of the total variability in the species data (45.9 % and 34.6 % for axis 1 and 2, respectively). The concentration of chl-a, the conductivity and the water level fluctuation seemed to have the most important influence on the temporal and vertical distribution of most of the zooplankton taxa (Table 9). Chl-*a* was the most important factor for the rotifers *K. longispina* and *Hexarthra* sp. and for the copepod *M. albidus*, in combination with the positive affection of the concentration of SiO_2. DO and pH affected mostly the rotifers *C. unicornis* and *Keratella quadrata*, as well as the cladoceran *Daphnia cucullata*. Moreover, DO and pH were negatively related to conductivity which seem to have played an indirect role for the above three species. There was a strong positive correlation of the water level (WL) and of temperature with *Collotheca* sp. and *D. blanci* larvae. Among the other parameters, transparency was the most important factor for *Filinia longiseta*, while the nutrients PO_4, NO_3 and NO_2 had always less important effect in the species variability (Table 2).

Table 8. Correlations of zooplankton species in Lake Trichonis with environmental factors such as temperature, DO, conductivity, pH, PO_4, NO_3, NO_2, NH_4, SiO_2 and Chl-a with the first two CCA axes, eigenvalues of the ordination axes and sum of all unconstrained eigenvalues (total inertia) for CCA analysis

Environmental variable	Axis 1	Axis 2
Temperature	-0.216	-0.807
Dissolved Oxygen	-0.387	0.331
pH	-0.156	-0.346
Conductivity	-0.026	-0.029
PO_4	0.289	-0.003
NH_4	-0.114	0.132
NO_2	-0.369	0.265
NO_3	0.322	0.176
SiO_2	0.280	0.065
Chl-a	-0.340	0.553

Axes	1	2	Total inertia
Eigenvalues	0.320	0.135	1.982
Species-environment correlation	0.805	0.877	
Cumulative percentage variance			
of species data	16.1	23.0	
of species-environment relation	43.6	62.0	

Sum of all eigenvalues	1.982
Total inertia:	0.734

Finally, the results of the CCA analysis in Stratos Reservoir indicate that the water flow (expressed as the water retention time) and temperature, as well as oxygen and conductivity can play an important role in the seasonal variation of various zooplankton species.

The first two axes used in the ordination diagram (Figure 8) explain 55.2 % of the total variability in the species data (32.6 % and 17.8 % for axis 1 and 2, respectively) in Stratos Reservoir (Table 10). Water retention time (WRT), as well as temperature, were among the most important factors affected various zooplankton species and especially the most abundant cladocerans *B. longirostris, D. cucullata, C. pulchella* and in a smaller degree *D. orghidani*.

Table 9. Correlations of zooplankton species in Lake Amvrakia with environmental factors such as water level (WL), temperature, DO, conductivity, pH, transparency, PO_4, NO_3, NO_2, NH_4, SiO_2 and Chl-a with the first two CCA axes, eigenvalues of the ordination axes and sum of all unconstrained eigenvalues (total inertia) for CCA analysis

Environmental variable	Axis 1	Axis 2
Temperature	-0.242	0.194
pH	-0.317	-0.342
Conductivity	0.177	0.514
Dissolved Oxygen	-0.060	-0.310
NO_3	-0.175	0.140
NO_2	-0.198	-0.058
NH_4	-0.238	0.168
SiO_2	0.462	0.059
PO_4	0.088	0.040
Chl-a	0.759	-0.152
Transparency	0.364	0.118
Water Level	-0.400	0.365

Axes	1	2	Total inertia
Eigenvalues	0.459	0.346	2.565
Species-environment correlation	0.902	0.768	
Cumulative percentage variance			
of species data	17.9	31.4	
of species-environment relation	40.9	71.7	

Sum of all eigenvalues	2.565
Total inertia:	1.122

Conductivity along with chl-a were also affected the rotifers *K. cochlearis* and *G. stylifer*, but reversely correlated with *Synchaeta* sp. and Bdelloidea, while the two former parameters affected also the mollusk larvae of *D. blanci* (only in the second sampling year). Temperature and conductivity was reversely related to DO, which exercised exactly the opposite effect on the above rotifer species. There was a strong correlation of DO with the copepods *Eudiaptomus drieschi* and *Macrocyclops albidus* and with their nauplii, as well as with the rotifers *Polyarthra* sp. and *Asplanchna priodonta*. Among the chemical parameters, the nitrates correlated with *K. cochlearis* and *G. stylifer*, while the ammonia was related with the presence of the rare species *Canthocamptus* sp., *Limnocalanus macrurus* and *Alona* sp., which were found mainly during the first sampling year (Figure8).

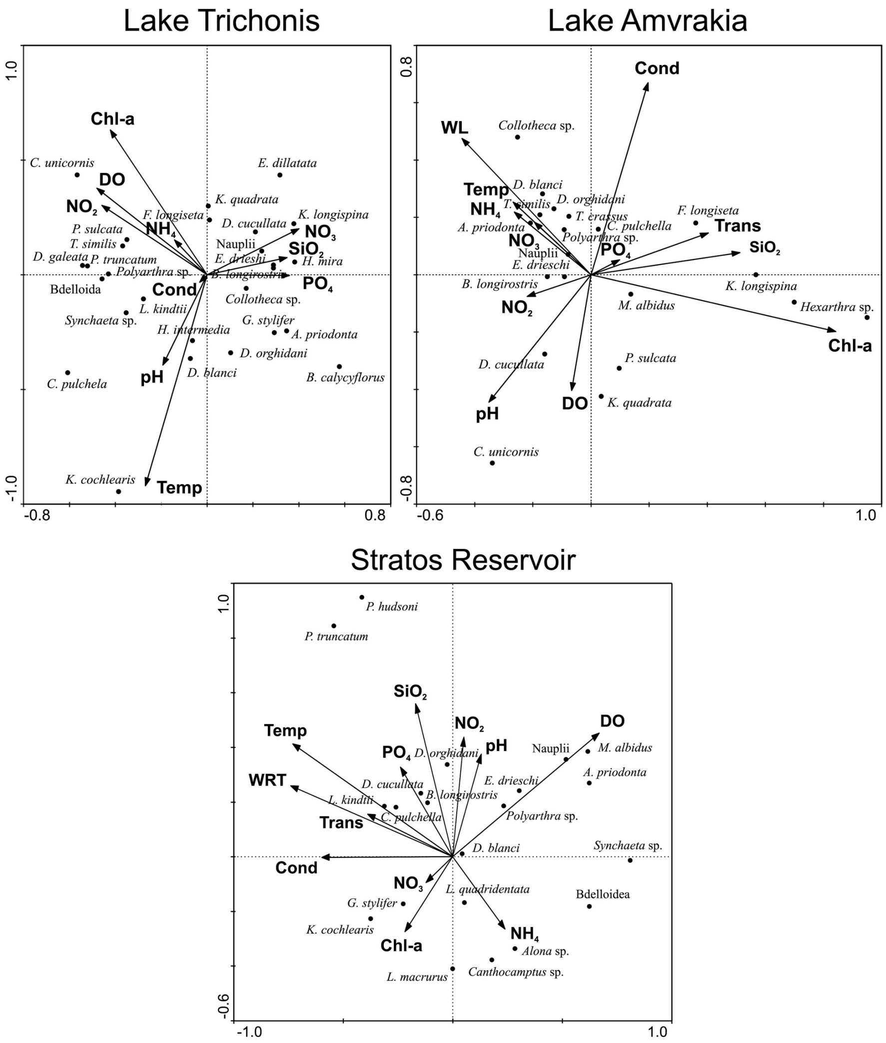


Figure 8. Canonical Correspondence Analysis (CCA) biplot ordination diagram of the first two canonical axes with the most important zooplankton species (Δ) and the environmental variables (arrows). Environmental parameters are abbreviated as: *Temp*, temperature; *Cond*, conductivity; *DO*, dissolved oxygen; *Chl*-a, chlorophyll-a concentration; *WL*, water level; *WRT*, water retention time.

Table 10. Correlations of zooplankton species in Stratos Reservoir with environmental factors such as water retention time (WRT), temperature, DO, conductivity, pH, transparency, PO_4, NO_3, NO_2, NH_4, SiO_2 and Chl-a with the first two CCA axes, Eigenvalues of the ordination axes and sum of all unconstrained eigenvalues (total inertia) for CCA analysis

Environmental variable	Axis 1	Axis 2
Temperature	-0.696	0.388
DO	0.639	0.425
Conductivity	-0.569	-0.002
pH	0.125	0.353
Transparency	-0.369	0.146
PO_4	-0.227	0.309
NO_3	-0.116	-0.089
NO_2	0.050	0.412
NH_4	0.229	-0.250
SiO_2	-0.161	0.527
Chl-a	-0.207	-0.258
WRT	-0.705	0.244

Axes	1	2	Total inertia
Eigenvalues	0.357	0.195	1.095
Species-environment correlation	0.902	0.941	
Cumulative percentage variance			
of species data	32.6	50.4	
of species-environment relation	46.7	72.2	

Sum of all eigenvalues	1.095
Total inertia:	0.765

The influence of the environmental parameters in the zooplankton species has been also investigated in Lakes Lysimachia and Ozeros using multiple regression analysis (Chalkia and Kehayias, 2013a; 2013b). The results for these two lakes showed that temperature was the crucial element for the zooplankton variation, followed by DO and pH, while the concentration of SiO_2 and conductivity were having lesser influence.

Consequently, the investigation of the influence of the environmental parameters on the variation of zooplankton in the five lakes revealed that the temperature and DO were the most important elements. Temperature is considered to be a crucial factor influencing many aspects of the biology and ecology of the zooplanktonic organisms (Wetzel, 2001). In the present study temperature played an important role for several rotifer and cladoceran species. It has been reported that temperature affects the metabolic rate of cladocerans and their occurrence and distribution (Moore et al., 1996; Huber et al., 2010) and exercises strong influence on rotifer species (Hoffmann, 1977; Akbulut et al., 2008).

Oxygen concentration is considered among the most important abiotic parameters affecting the zooplankton along the vertical axis of the aquatic ecosystems, since most of these organisms tend to avoid living in hypoxic or anoxic conditions and remain restricted in the well oxygenated parts of the water column (Żurek, 2006). However, in the present study a considerable number of specimens from all the zooplankton groups were recorded even in the deeper layer (35–40 m) of lakes Trichonis and Amvrakia, which at the end of stratification period was hypoxic and even anoxic in the latter lake. The persistence of freshwater planktonic animals to hypoxia and anoxia is less well known and today is an interesting aspect given the increase of the hypoxic/anoxic basin worldwide (Diaz, 2001; Vanderploeg et al., 2009).

Chlorophyll-a seemed to be one of the major affecting parameters for the zooplankton herbivores in lakes Trichonis and Amvrakia, which are considered oligo-mesotrophic and mesotrophic, respectively. This could be explained considering that most of zooplankton organisms could be greatly depended on phytoplankton biomass (as represented by chl-*a* concentration) for their energy demands, especially in these ecosystems of lower trophicity.

Conductivity was among the major environmental variables influencing zooplankton in Lake Amvrakia, similarly to what have been reported by others in other sulfur lakes of Europe (Stanković et al., 2010; Bielańska-Grajner and Gładysz, 2011). The influence of conductivity to zooplankton is probably the result of the high concentration in sulphates in the water, which can reduce filter-feeding rate in cladoceran species. The above could explain the negative correlation of conductivity with the cladoceran *D. cucullata*, although more research on that issue would be required.

Flow intensity, expressed as WRT, was suggested to be among the most important determinants of seasonal events in tropical reservoirs (Gliwicz, 1999). This parameter can have indirect influence to the zooplankton organisms by affecting other physicochemical parameters such as temperature, DO, transparency, conductivity and the concentrations of nutrients. Furthermore, water level (WL) fluctuations are expected to exercise several indirect influences to the biotic elements affecting the total nutrient load within the lake, and consequently the chl-a. This must has been the reason why WL and chl-a concentration presented opposite trends in Lake Amvrakia (Figure 8). Water level measurements in this lake showed great variation between the two years of study and turned to have some considerable effects in the abundance of *D. blanci* larvae, by the habitat reduction of its adult forms and the diminishing of the overall reproductive capacity of the population, as previously discussed.

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Chapter 5

ZOOPLANKTON OF THE COOLING RESERVOIR OF THE BELOYARSKAYA NUCLEAR POWER STATION: SPECIES CHARACTERISTICS AND ACCUMULATIVE ABILITY

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ABSTRACT

This chapter reports the results of an extended investigation (1986–2011) on the state of the zooplankton complex and its capacity to accumulate radionuclides and microelements in the Beloyarskoye reservoir – the cooling reservoir of the Beloyarskaya nuclear power station in the Middle Urals. The zooplankton species composition, abundance and biomass were investigated in four zones of the reservoir: the heated water discharge zone, the discharge and water intake channels,

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the control region and the central water area. In the observation zones the investigated parameters were different. Thus, in Teplyi Bay and in the discharge channel adjacent to the power station the abundance and biomass of zooplankton were much lower after its entrance through the cooling system of the station. The analysis of mortality among the predominant species evidenced of the greater sensitivity to injuring factors of copepods in comparison to cladocerans. The main attention was paid to the water discharge channel through which low-radioactive water was discharged into the cooling reservoir. The quantity of radioactive pollutants entering the cooling reservoir together with zooplankton was estimated. The investigation of the accumulation levels of ^{90}Sr and ^{137}Cs in the zooplankton, as well as in other hydrobionts and in the sediment, showed considerably higher accumulation coefficients in the case of phyto- and zooplankton in comparison to fish species, mollusks and the sediment. The accumulation coefficients of 70 chemical elements in the zooplankton ranged from 10^2 to 10^7. A significant positive correlation between the concentrations of chemical elements in zooplankton and the water medium indicated that zooplankton generally reflected the chemical composition of its habitat and responds quickly to changes in the chemical composition of the water. Thus, zooplankton can be considered as a highly sensitive biogeochemical indicator of water pollution with heavy metals and radionuclides.

INTRODUCTION

Nuclear power stations are big industrial enterprises which can influence the state of the water bodies being close to them and serving as their cooling reservoirs. In normal operation of a nuclear power station, there are three kinds of affection in these cooling reservoirs, such as radiation, chemical and thermal pollution. The effect of radiation lies to the receipt of small amounts of low-level radioactive substances, which are quickly absorbed by hydrobionts and sediments. In zones of the low-level radioactive water discharge the radiation effect is often manifested along with the combined effect of heated water and mechanical injury of small organisms. Power stations can also be a source of chemical pollution of cooling reservoirs due to construction works. All these factors together can reduce the resistance of hydrobionts and cause various synergistic effects (Chebotina et al., 1992; Egorov, 2007).

The combined effect of various factors can be estimated by the methods of bioindicative analysis based on the changes in the structural characteristics of the aquatic communities (Krylov, 2012; Pashkova, 2012). Zooplankton is an important component of the freshwater ecosystems and it is consisted of a large number of small invertebrates, the composition of which vary depending on various ecological factors – temperature, light regime, time of the day, season, habitat, water chemical composition, etc. Zooplankton organisms have a large total body surface, from which they can absorb radionuclides and chemicals entering the water, and therefore, they can be used as indicators of pollution of the aquatic ecosystem in the areas of nuclear power stations (Chebotina et al., 2002). The existing literature on the zooplankton deals with various aspects of biology and ecology, however, issues concerning the accumulation of chemical and especially radioactive contaminants by these organisms are still insufficiently studied.

In this chapter we present the results of an extended investigation (1986–2012) of the zooplankton community in the cooling reservoir of the Beloyarskaya Nuclear Power Station (BNPS) in the Middle Urals, focusing on species characteristics and their accumulative ability of contaminants.

THE STUDY AREA

The Beloyarskoye reservoir is an artificial reservoir formed in 1959-1963 on the Pyshma River (Figure 1). The river belongs to the Ob-Irtysh basin and is a right tributary of the Tura River flowing into the Tobol, a tributary of the Irtysh River. The Pyshma River rises from the Lake Klyuchevskoye near the town of Verkhnya Pyshma. The total length of the river is 626 km and its catchment area is 19400 km^2. The flow rate during the low water period is 0.5-0.7 m/sec, the width in the upper part is 8-10 m, and closer to its mouth it reaches 60-100 m.

The Beloyarskoye reservoir is used as a cooling reservoir of the Beloyarskoye Nuclear Power Station (BNPS), the first big nuclear power station in the world, which was put into operation in 1964. At the first stage of the BNPS construction the first and second power units were built with Uranium-graphite reactors of the channel type AMB–100 and AMB–200. The first unit was taken out of operation in 1981, while the second one has been operated from 1967 to 1989. The third power unit with the fast neutron shell-type liquid-metal-reactor (BN–600) was put in operation in 1980 and is still working, while the construction of the fourth unit is being completed.

The plant species composition in the Beloyarskoye reservoir is the following: algae – *Cladophora fracta* Kütz., *C. glomerata* (L.) Kütz., *Spirogira* sp., *Hydrodiction reticulatum* Lagerch.; higher plants (immersed):

Elodea canadensis Rich., *Ceratophyllum demersum* L., *Myriophyllum spicatum* L., *Potamogeton perfoliatus* L., *P. compressus* L., *P. pectinatus* L., *P. crispus* L., *P. natans* L., *P. lucens* L., *Ranunculus circinatus* Sibth., *Stratiotes* aloides L.; plants floating on the surface: *Lemna minor* L., *L. trisulca* L., *Hydrocharis morsus ranae* L.; riverside water plants: *Alisma plantagoaquatica* L., *Typha latifolia* L., *Cicuta palustris* L., *Calla palustris* L., *Scirpus lacustris* L., *Bidens tripartica* L., *Equisetum limosum* L., *Rumex confertus* Willd., *Phragmites communis* Trin., *Geum rivale* L., *Carex* sp. In the heated water discharge area nine plant species have been recorded: *C. glomerata*, *C. fracta*, *Spirogira* sp., *E. canadensis*, *C. demersum*, *L. minor*, *P. pectinatus*, *T. latifolia*, *Carex* sp., *P. lucens*, *H. morsus ranae*. Since 1986 the abundance of *C. demersum*, *L. minor* has increased, while of *E. canadensis* has decreased.

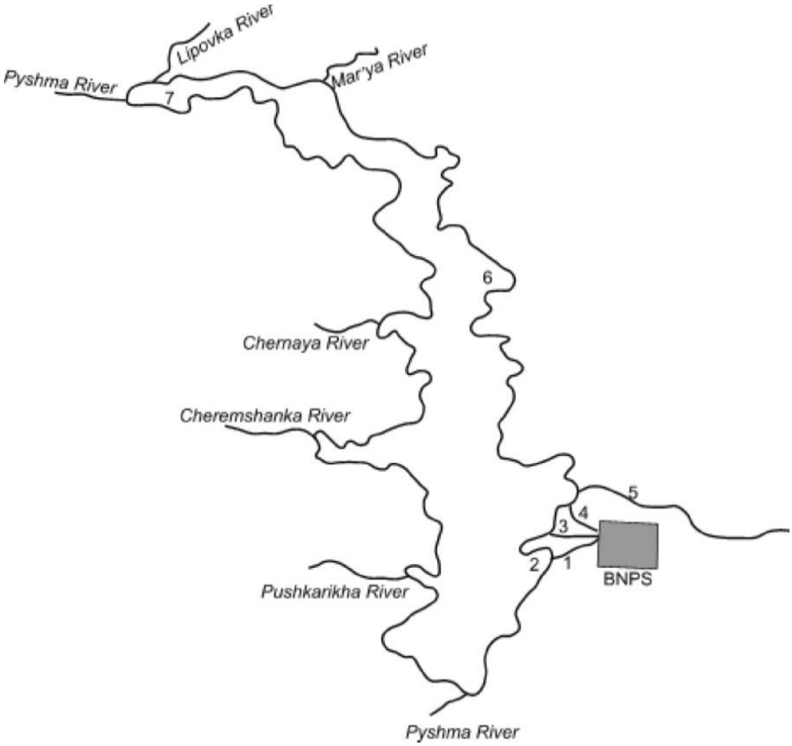

Figure 1. Map of the Beloyarskoye reservoir. 1: water discharge channel, 2: Teplyi Bay, 3: water intake channel, 4: SWD channel, 5: bypass channel, 6: Shchuchii Bay, 7: the upstream part of the reservoir.

The fish fauna of the reservoir consists mainly of the species *Rutilus rutilus lacustris* Pall., *Abramis brama* L., *Esox luciu* L., *Cyrpinus carpio* L., while less common are the species *Perca fluviatilis* L., *Tinca tinca* L., *Carassius auratus gibeli* Bloch and *Lucioperca lucioperca* L. Among phytoplankton organisms, Chlorophyta (Chlorococcaceae, Desmidiaceae, Volvocaceae) species predominate. Bacillariophyta, Cyanophyta, Euglenophyta, Pyrophyta are less spread. Zooplankton is represented mainly by crustaceans (copepoda and cladocera) while the number of rotifer species is small.

The sediments of the Beloyarskoye reservoir are predominantly silt, less common are submerged soil, sandy-silt, silty-sand and sand grounds. Sand grounds are typical for the shallow coastal zone and the bottom in the deep part is covered mainly with silty sapropel. Currently, the reservoir can be classified as a calcium hydrocarbonate water body with a medium mineralization level and normal oxygen conditions. The presence of a zone with an increased water temperature and slightly alkaline medium creates favorable conditions for fish and other aquatic organisms.

ZOOPLANKTON COLLECTION AND ANALYSIS

The zooplankton species composition, abundance, biomass and accumulation ability were investigated in four areas within Beloyarskoye cooling reservoir (Figure 1). These areas were: the heated water discharge zone, the control region, the water discharge and intake channels and the central water area of the reservoir. To determine the species composition, abundance and biomass, zooplankton samples were collected with conical nets made of bolting cloth no. 70, and put in 40 % formalin solution. Samples were collected from June to October in 1986-2011. Each sample was transferred to a Petri dish, and the species identification was determined under a binocular microscope. The abundance of each species was determined in Bogorov chambers under a binocular microscope. To measure the biomass of zooplankton the average size of males and females of each species was estimated, while for the younger specimens calculations were made separately. The biomass was calculated from tables using body length measurements per raw mass of one specimen (Manuylova, 1964; Kutikova, 1970; Alekseyev, 1995).

To determine the content of radionuclides, zooplankton samples were collected simultaneously with sampling for the species biomass estimation from the upper water layer (0–1.5 m) by trawling from a boat, using conical nets made of bolting cloth no. 21. After the water was drained off from each sample, zooplankton wet mass was weighed, dried and burned in a muffle furnace at 450 °C. The content of ^{137}Cs in the ash samples was determined using a scintillation γ-spectrometer and "Progress" software, while ^{90}Sr was determined by the radiochemical method, using a low background LBD-2000 device. The statistical error of measurements did not exceed 10–15 %.

To analyze the content of trace elements we sampled zooplankton in the SVD channel outlet area in June-July 2010-2011. For the accumulation analysis of trace elements, the zooplankton samples were first pulverized using an electric mill. The powdered samples were dissolved in a mixture of nitric, hydrochloric and hydrofluoric acids in the ratio of 2:1:1 and heated in an autoclave for 15–30 min at temperatures of 150-160 ºC. Quantitative estimations of the elements were made using a mass spectrometer (Perkin-Elmer SCIEX, Canada, U.S.) with a calibration standard solution for the required concentration range of the elements. The relative standard error did not exceed 10–20 %. All data accounted for the dry mass of zooplankton.

ZOOPLANKTON SPECIES COMPOSITION, ABUNDANCE AND BIOMASS IN THE DIFFERENT ZONES

1) The Heated Water Discharge Zone and the Control Area

The temperature of the water medium is an important abiotic factor affecting the ecosystem structure and metabolism of the inhabiting organisms. In the area of the heated water discharge hydrochemical and hydrobiological characteristics are changed. Thus, the concentration of organic substances increases, along with the oxygen demand for their oxidation. As a result oxygen concentration in the water is reduced. Concentrations of biogenic elements and mineralization of the water also change (Suzdaleva and Beznosov, 2000; Egorov, 2001; Vitsbiskas, 2002). Alteration of the temperature conditions causes changes in the composition, structure and other characteristics of the aquatic communities: the abundance of cold-loving species decreases, some of them disappear partly or totally, either they resettle in colder parts of the reservoir, or some of them adapt to the new environment conditions. In these areas, the ratio of species-indicators of saprobity change, while warm water often reduces species diversity with eurythermal species becoming the base of zooplankton communities (Pashkova, 2009; Protasov et al., 2011).

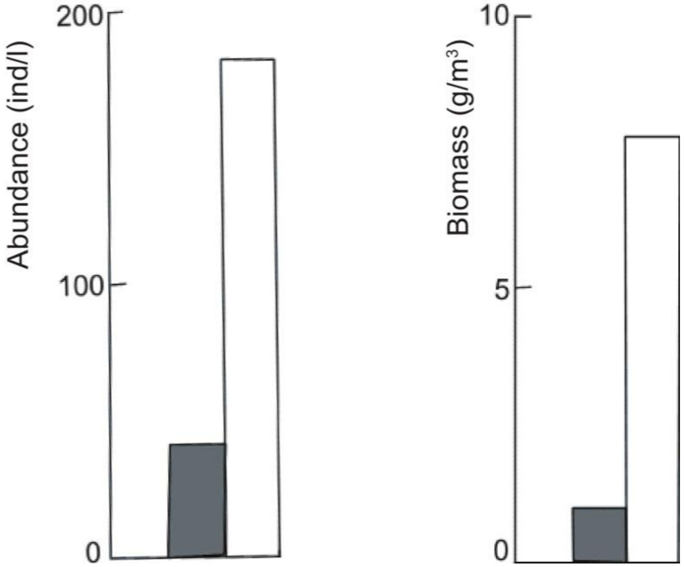

Figure 2. Total abundance and biomass of zooplankton in Teplyi Bay (black bars) and Shchuchii Bay (light bars) of the Beloyarskoye reservoir (average values).

To assess the impact of the discharged heated water on the zooplankton community composition, abundance and biomass, two sampling sites were selected; Teplyi Bay being within the heated water discharge zone and Shchuchii Bay being in the control area, which was located 7 km upstream of the latter (Figure 1). From June to August in 1986 and in 1988 zooplankton abundance ranged from 14 to 107 ind/l in Teplyi Bay and from 18 to 328 ind/l in Shchuchii Bay, while biomass varied between 0.4–2.4 and 1.2–25.8 g/m^3, respectively. On average, the abundance and the biomass of zooplankton in Shchuchii Bay were 4 and 7 times higher respectively, than in Teplyi Bay (Figure 2). Indeed, statistical analysis revealed significant differences (t-test, $p < 0.05$) in the abundance and biomass of zooplankton between these two areas. This fact indicates the negative affection of the heated water from the BNPS to the zooplankton abundance and biomass, since in Teplyi Bay being adjacent to the power station, both parameters were lower compared to Shchuchii Bay being in an area of no affection. Other authors come to similar conclusions evidencing that zooplankton abundance depends on the temperature of the water medium (Makarevich and Ishkulov, 2010).

In both areas, crustaceans noticeably prevailed over rotifers both in abundance and biomass. Thus, in the heated zone the average abundance of crustaceans was 25 ind/l and of rotifers 7 ind/l in all sampling occasions, while the respective biomass values were 1.1 and 0.01 g/m^3. In Shchuchii Bay the average abundance of crustaceans and rotifers were 109 ind/l and 15 ind/l and their biomass was 8 and 0.07 g/m^3, respectively. The younger stages of crustaceans accounted for 4 - 88 % of the total zooplankton in various sampling periods. Generally, the abundance of juveniles was also significantly lower in the heated water zone (Teplyi Bay) than in Shchuchii Bay.

The cladoceran *Daphnia pulex* predominated in both areas. Among the other species, *Eudiaptomus graciloides*, *D. cristata*, *Bosmina kessleri*, *Chydorus sphaericus*, *Diaphanosoma brachyurum* and *Cyclops vicinus* predominated in biomass in different periods.

The abundance and biomass of the numerically most important species in the reservoir were appreciably variable depending on many factors, including the season of sampling, the temperature of the water medium, the sampling area, etc. In particular, it was noted that in Teplyi Bay in July 1986 at an average water temperature of 20 ºC the cladoceran *D. pulex* predominated and reached 71 % of the total zooplankton biomass, while at 30 ºC the cladoceran *D. cristata* accounted for 31 %, *B. kessleri* for 23 % and *Ch. sphaericus* for 22 %. At the same time in Shchuchii Bay with an average temperature of 16 ºC, *D. pulex* and *D. cristata* predominated and accounted for 49 % and 20 %, respectively, while at an average temperature of 26 ºC, the respective proportions of *D. pulex*, *D. brachyurum* and *D. cristata* were 32 %, 28 % and 25 %. At the same water temperature in various summer months the composition of predominating zooplankton species also changed. For example, in Teplyi Bay at an average temperature of 29.5 º C in July 1988 *D. pulex* and *E. graciloides* predominated (63 % and 27 %, respectively), while in August at the same temperature *D. cristata* (31 %), *B. kessleri* (23 %) and *Ch. sphaericus* (22 %) were the most abundant species. In Shchuchii Bay at an average water temperature of 20 ºC both in June and in August, the composition of the dominant complex varied with *E. graciloides* accounting for 47 % and *D. cristata* for 32 % in June, while in August *Ch. sphaericus*, *D. brachyurum* and *D. cristata* accounted for 35, 29 and 23 %, respectively. In July 1986 at the same temperature (19 ºC) in Teplyi Bay there was only one dominant species *D. pulex* (71 %), while at the same time in Shchuchii Bay there were two dominant species *D. pulex* (41 %) and *D. cristata* (42 %).

The above-mentioned differences in the abundance and biomass of the whole zooplankton community in Teplyi Bay and Shchuchii Bay were also marketed in the abundance and biomass of the predominating forms of zooplankton. In particular, the abundance and biomass of *D. pulex* and *D. cristata* were 8–10 times higher in Shchuchii Bay compared with the heated zone, while the respective values of *E. graciloides* were 6 times higher. We emphasize that zooplankton is more sensitive towards the temperature factor compared to phytoplankton (Chebotina and Guseva, 2006).

2) Water Intake and Water Discharge Channels

Among the important effects of nuclear power stations on the ecosystems of their cooling reservoirs is the injury of the hydrobionts as they pass along with water through the cooling system. The pumped water containing zooplankton is subject of significant pressure and high velocity in the tubes of the condenser, at the water discharge channels and in their open parts. Despite a short period of staying in the power station (approx. 8 min), organisms are subjected to mechanical injury and thermal shock caused by rapid temperature rise (up to 90 °C). Besides, before entering the cooling system the water is chlorinated to prevent bacterial and fungal overgrowth of the inner tube surface (Mordukhai-Boltovskoy, 1975).

The results of the investigation of samples taken before and after the water passage through the cooling system showed that zooplankton in the intake and discharge (warm) channels accounted for 17 and 16 species, respectively. It can be assumed, then, that water passage through the cooling system had no significant effect on the total number of zooplankton species. However, the abundance and biomass of the total zooplankton considerably decreased after passage through the cooling system, being three times and two times lower, accordingly, while similar were the findings for some of the zooplankton groups. These differences were recorded in different years of observations (Juny 1987-Yuly 1991) (Figures 3, 4). The decrease of biomass after the passage through the cooling system was greater in the case of copepods (71 %) than of cladocerans (48 %) and this was statistically confirmed (t-test, $p < 0.02$). At the same time, the decrease of biomass in crustaceans (ca. decreased 53 %), their younger specimens (ca.73 %), and also in rotifers (ca. 53 %) was not statistically significant.

The zooplankton community in the zones of the water intake and discharge channels was represented by copepods (*E. graciloides*) and cladocerans (*D. cristata*, *D. cucullata*, *D. pulex, D. brachyurum*, *B. longirostris*).

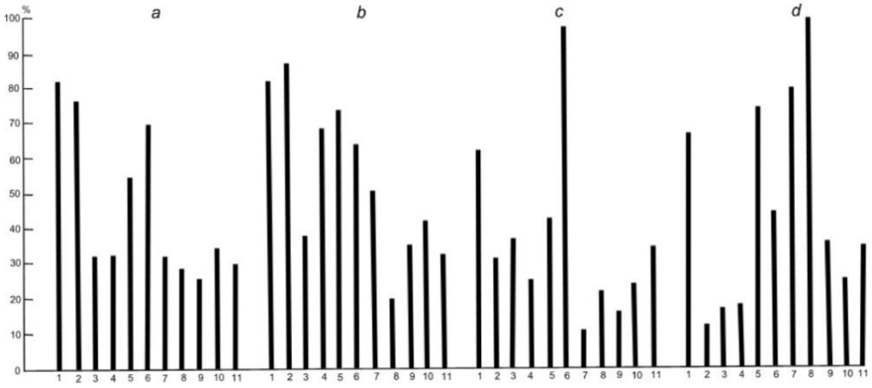

Figure 3. The % decrease of abundance of total zooplankton (*a*), cladocerans (*b*), copepods (*c*) and rotifers (*d*) in the water discharge channel in comparison to the water intake channel measurements. Sampling points in various seasons: 1 – 06.1987; 2 – 07.1987; 3 – 08.1987 ; 4 – 10.07.1990; 5 – 17.07.1990; 6 – 24.07.1990; 7 – 31.07.1990; 8 – 9.07.1990; 9 – 16.07.1991; 10 – 23.07.1991; 11 – 30.07.1991.

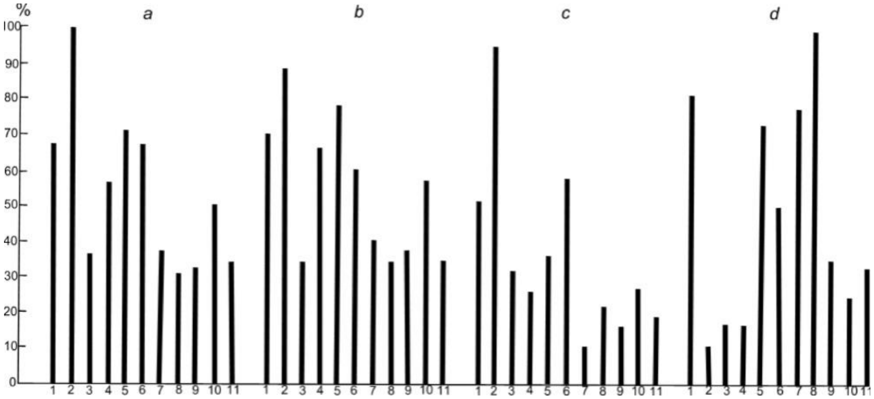

Figure 4. The % decrease of the biomass of the total zooplankton (*a*), cladocerans (*b*), copepods (*c*) and rotifers (*d*) in the water discharge channel in comparison to the water intake channel measurements. Sampling points in various seasons: 1 – 06.1987; 2 – 07.1987; 3 – 08.1987 ; 4 – 10.07.1990; 5 – 17.07.1990; 6 – 24.07.1990; 7 – 31.07.1990; 8 – 9.07.1990; 9 – 16.07.1991; 10 – 23.07.1991; 11 – 30.07.1991.

There were statistically significant differences (t-test, $p < 0.02$) in the biomass decrease between the two most important crustaceans in the region, such as the copepod *E. graciloides* (biomass decreased by 72 ± 6 %) and the cladoceran *D. cristata*, (biomass decreased by 40 ± 9 %) after their passage through the cooling system. Besides, there were great differences (t-test, p <

0.02) in the biomass decrease between the copepod *E. graciloides* and the dominant cladocerans (*D. cristata, D. cucullata, D. pulex, D. brachyurum, B. longirostris*). Their average biomass decline was 49 ± 4 %. Thus, the analysis of mortality of the dominant species after their passage through the cooling system showed that copepods were more sensitive to damaging factors than cladocerans.

It has been calculated that about 11 tons of zooplankton daily pass through the water intake channel. According to the above results, a proportion of approximately 45 % (5 tons/day) of this zooplankton returns alive to the reservoir through the discharge channel, while the remaining 55 % of the organisms (6 tons/day) decease. Thus, during the entire summer-autumn period the cooling system of the BNPS is responsible for the elimination of about 720 tones of zooplankton.

3) Sewage Water Discharge Channel (SWD Channel)

A partial entry of liquid discharge (waste water, storm and melt water) into the cooling reservoir is through the SWD channel. Water is discharged to this channel from the power station and the adjacent Institute of Reactor Materials (IRM), were an experimental reactor is working (Koltik, 2001). During the investigation in June-July 2005, nine zooplankton species were found in the SWD channel, whereas in the control area – the upstream part of the reservoir – 22 species were present. The abundance and biomass of zooplankton in the SWD channel were significantly lower compared to the control area, located about 15 km upstream from the power station (Table 1). This evidences of the oppression of zooplankton by the water discharged from the SWD channel (Figure 5). Thus, the upstream part, which receives nutrients with the Pyshma River, is more favorable for the development of zooplankton than the SWD channel.

These two areas differed also in the zooplankton community composition. In the control upstream part of the reservoir the community was consisted mainly by cladocerans and copepods, while in the SWD rotifers prevailed (Table 1). Moreover, the community in the control upstream part of the reservoir was consisted mainly by cladocerans and copepods in similar proportions, whereas in the SWD channel the abundance of cladocerans was considerably lower than of copepods (Table 1). The dominant species were also different.

Table 1. Abundance and biomass of the main zooplankton groups in the SWD channel and the upstream part of the reservoir

Zooplankton Group	Abundance (ind/l)		Biomass (g/m^3)	
	SWD channel	Upstream part	SWD channel	Upstream part
Crustaceans:				
cladocerans	3.4	51.3	0.38	3.36
copepods	23.4	60.3	0.88	3.24
Rotifers	38.4	19.9	0.02	0.09

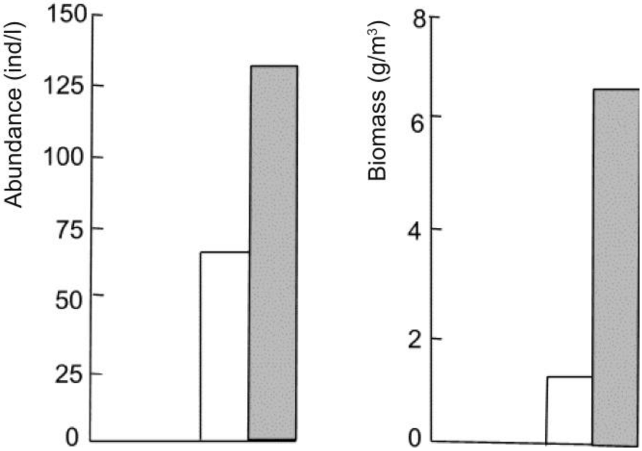

Figure 5. The total abundance and biomass of zooplankton in the SWD channel (light bars) and in the upstream part of the Beloyarskoye reservoir (black bars).

In the upstream part the most abundant species were the cladocerans *B. kessleri* (13 % of the total zooplankton), *B. obtusirostris* (9 %) and *D. brachyurum* (10 %), the copepod *Macrocyclops albidus* (8 %) and the rotifer *Keratella quadrata* (8 %). In the SWD channel the rotifers *K. quadrata* and *K. cochlearis* predominated in the zooplankton (30 % and 22 %, respectively). Considering the biomass, the copepod *M. albidus* and the cladoceran *B. obtusirostris* prevailed in the upstream part (38 % and 23 % of the total biomass of zooplankton, respectively), while in the SWD channel zone the copepods *Eucyclops serrulatus* (37 %) and *E. graciloides* (28 %) and the cladoceran *Leptodora kindtii* (21 %) predominated.

4) The Central Part of the Reservoir

The zooplankton abundance in the central part of the reservoir in different observation periods (June-August 1989) varied from 19 to 471 ind/l (average: 131 ind/l) and its biomass varied from 0.3 to 19 g/m^3 (average: 5 g/m^3). As in the bays of the cooling reservoir, crustaceans significantly prevailed over the rotifers in most cases. A large number of juvenile crustaceans (5 to 82 % of total zooplankton, depending on the time and site of observation) were recorded, while their biomass accounted for only 0.1–5 % of the total zooplankton.

The central part of the reservoir was subdivided into three zones: upper, middle and lower. In all zones the abundance and biomass of zooplankton in the periods of the highest water temperature (July) were higher than in colder autumn. The highest abundance and biomass of zooplankton was recorded in the upper zone in comparison to the lower one. In particular, at certain observation periods, zooplankton biomass was about 5–10 times greater in the upper zone than in the middle and lower. The differences between the upper and the lower zones were evidently connected with the Pyshma River, which brinks to the upper zone waste water from the cities of Ekaterinburg, Berezovsky and Verkhnya Pyshma with additional amounts of chemical elements and organic matter, thus stimulating the development of higher density of phytoplankton and consequently zooplankton organisms.

ACCUMULATION OF RADIONUCLIDES AND TRACE ELEMENTS

The investigation on the accumulation of radioactive and stable elements by zooplankton is ecologically significant because it comprises the food for fish and is a link in the food chain, leading to humans. In addition, zooplankton participates in the biochemical transformation of various substances in the water and finally their transportation from the pelagic zone to the bottom sediments. Thus, zooplankton is able to remove radioactive and chemical pollutants from the water (Kulikov and Chebotina, 1988).

Among the areas of the reservoir, the SWD channel is mostly affected by the low-level radioactive nuclear waste. The assessment of concentrations of ^{90}Sr and ^{137}Cs in the zooplankton in the mouth of the SWD channel during the operation of the third power unit (July-Oktober 2004) showed that the accumulation levels of ^{137}Cs were much higher than those of ^{90}Sr. In particular, the content of ^{90}Sr varied from 83 to 224 Bq/kg dry mass (mean 139 ± 17 Bq/kg), while the content of ^{137}Cs varied from 2500 to 4600 Bq/kg (mean 3250 ± 250 Bq/kg). In comparison to these values, the concentration of ^{90}Sr in the zooplankton in Shchuchii Bay located at a distance of 7 km upstream was averagely 5.3 ± 1.1 Bq/kg, and that of ^{137}Cs was 7.3 Bq/kg. These data show a significant entry of the radionuclides to the reservoir through the SWD cannel.

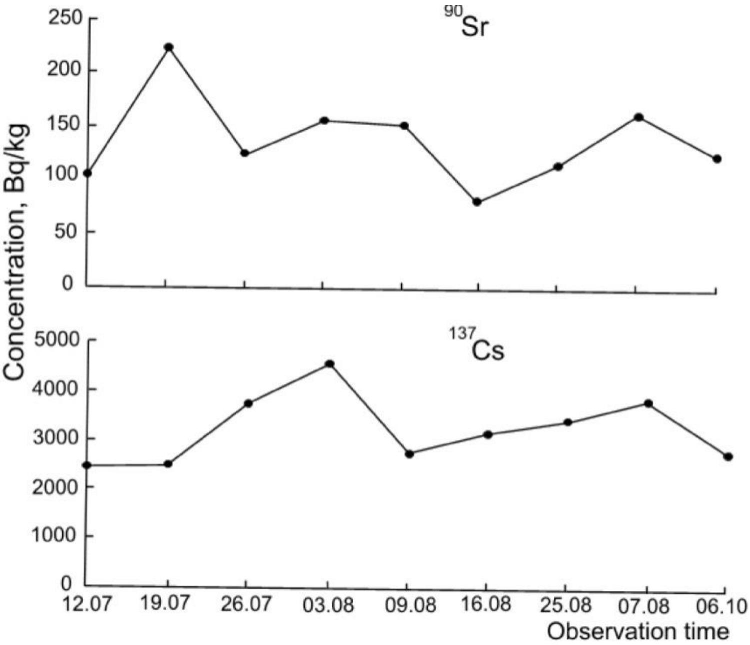

Figure 6. Concentrations of ^{90}Sr and ^{137}Cs in the zooplankton collected from the mouth of the SWD channel in different dates of observation.

The sediment of the reservoir is considered as the main depot for radionuclide accumulation (Kulikov and Chebotina, 1988), thus, it was interesting to compare the cumulative capacity of the sediment to the phyto- and zooplankton, as well as to other groups of hydrobionts sampled in the SWD channel. In this area, the concentrations of ^{90}Sr and ^{137}Cs varied slightly around the mean values during the investigation period (0.018 Bq/l and 0.016 Bq/l for ^{90}Sr and ^{137}Cs, respectively). On the basis of these data, accumulation coefficients (AC) were calculated for phyto- and zooplankton organisms, for the sediment, for some fish species (fry) and for mollusks. Accumulation coefficient is the ratio of the radionuclide concentration in hydrobionts and the sediment to its concentration in the water. The results revealed that ^{90}Sr accumulation coefficient for the sediment in the SWD channel was 1100 (Figure 6), while the respective values for the phytoplankton and zooplankton were 6-7 times higher (5850 and 6960, accordingly). Accumulation coefficients for the phyto- and zooplankton were also higher than those for fish (470–620) and mollusks (2120).

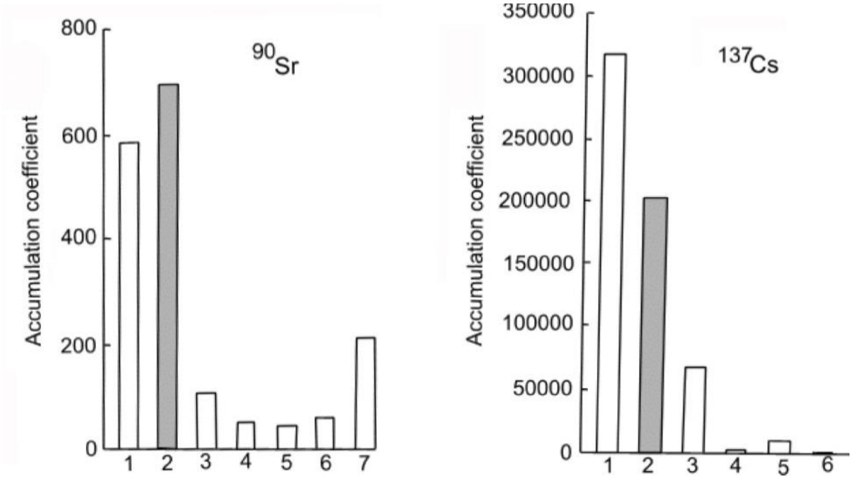

Figure 7. Comparative accumulation coefficients of ^{90}Sr and ^{137}Cs in hydrobionts and in the sediment from the mouth of the SWD channel: 1 – phytoplankton, 2 – zooplankton, 3 – sediment, 4 – the rudd (*Rutilus rutilus lacustris*), 5 – the loach (*Misgurnus fossilis*), 6 – the bream (*Abramis brama*), 7 – mollusks.

The accumulation coefficient for ^{137}Cs in the phytoplankton was 318620, which was 5 times greater than in the sediment (64060), while in the zooplankton reached 203190, being three times higher than in the sediment. In fish fry the accumulation coefficients were smaller and varied from 2170 to 9200. For mollusks, ^{137}Cs accumulation coefficients could not be calculated because the concentration was too low to be detected (Figure 7).

The SWD channel receives waste water from two sources, the nuclear power station and the Institute of Reactor Materials (IRM). We have evaluated the contribution of each enterprise to the contamination of zooplankton with ^{90}Sr and ^{137}Cs through the SWD channel (Figure 8). It was found that the power station contributed to zooplankton contamination more than IRM, especially with ^{137}Cs.

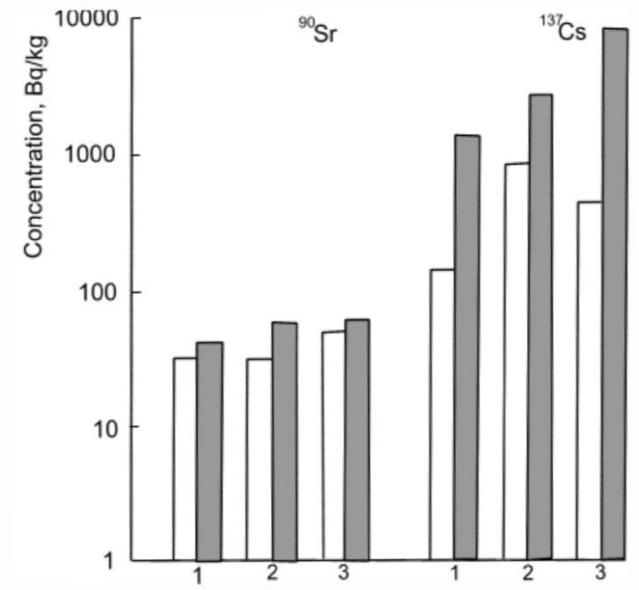

Figure 8. ^{90}Sr and ^{137}Cs concentrations in zooplankton from the SWD channel of the nuclear power station and IRM in different observation periods. 1 – 20.06.2005; 2 – 27.06.2005; 3 – 4.07.2005.

The zooplankton ability to accumulate 70 chemical elements, mostly as trace elements in the water media, was also estimated July 2011 in the SWD channel. The results showed that the concentrations of these elements varied within 10 orders of magnitude. The highest values were noted for Si (10^5–10^6 ppm/g dry mass), Mg, Al, Ca, Mn, Fe (10^4–10^5 ppm/g). They were followed in decreasing order by: Na, P, K, Ti (10^3–10^4 ppm/g), Sc, V, Ni, Cu, Br, Sr, Nb, Ba, Pb (10^2–10^3 ppm/g), Li , B, Co, Cr, Zn, Ga, As, Se, Rb, Zr, Y, Ag, Sn, Sb, La, Ce, Ta, W, Hg, U (10–10^2 ppm/g), Be, Mo, Cd, I, Cs, Pr, Nd, Sm, Gd, Dy, Er, Yb, Hf, Bi, Th (1–10 ppm/g), Ge, Pd, Eu, Tb, Ho, Tm, Lu, Ta , Re, Ti (1–10^{-1} ppm/g), Ru, Rh, In, Pt (10^{-1}–10^{-2} ppm/g), Ir, Te, Os, Au (10^{-2}–10^{-3} ppm/g (Chebotina et al., 2011).

A significant positive correlation between the concentrations of chemical elements in zooplankton and the water medium was marked (Figure 9). This relationship suggests that zooplankton reflects the chemical composition of its habitat. Indeed, since plankton almost instantly responds to changes in the chemical composition of the water, it can be recommended as a highly sensitive biogeochemical indicator of water pollution with heavy metals and radionuclides.

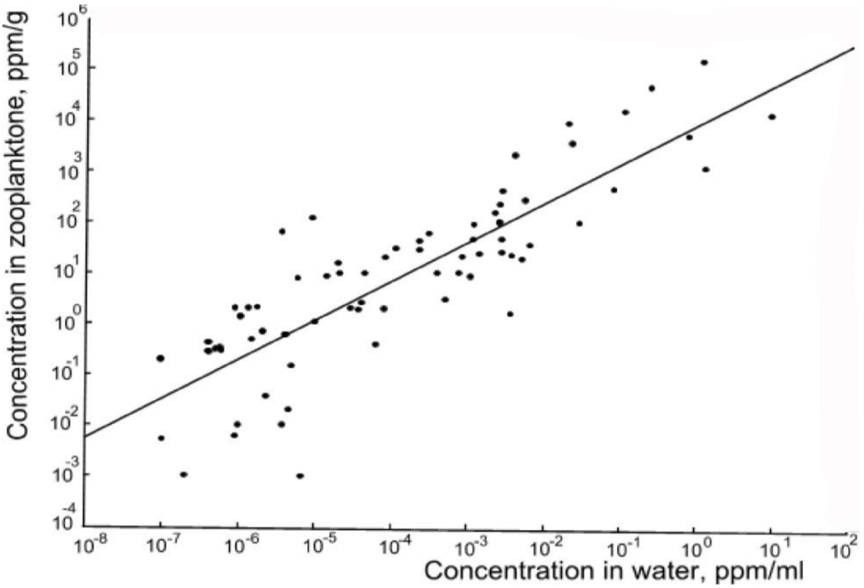

Figure 9. Correlation between concentrations of chemical elements in the zooplankton and in the water medium.

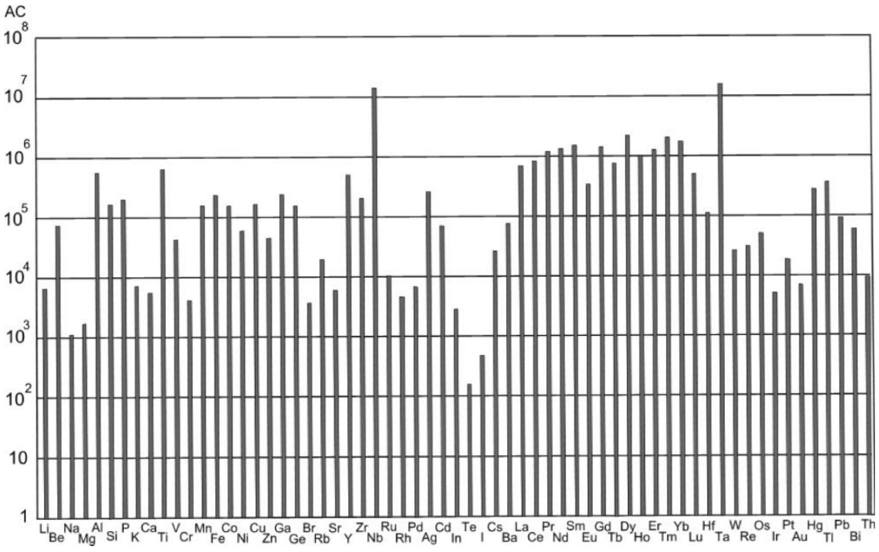

Figure 10. Accumulation coefficients of chemical elements in the zooplankton.

Table 2. List of 31 zooplankton species recorded in the cooling reservoir of Beloyarskaya nucler power station during 1986-2011

Class Crustaceans	
Cladocerans	
Alona rectangula Müll.	*Bosmina kessleri* Uljan.
Bosmina longirostris Müll.	*Daphnia cucullata* Sars.
Bosmina obtusirostris Sars.	*Daphnia pulex* Leydig.
Bythotrephes longimanus Leydig.	*Diaphanosoma brachyurum* Liev.
Ceriodaphnia quadrangula Müll.	*Leptodora Kindti* Focke.
Chydorus sphaericus Müll.	*Sida crystallina* Müll.
Daphnia cristata Sars.	
Copepods	
Acanthocyclops viridis Jur.	*Eudiaptomus graciloides* Lill.
Cyclops vicinus Uljan.	*Macrocyclops albidus* Jur.
Eucyclops serrulatus Fisch.	
Class Rotifers	
Asplanchna priodonta Gosse.	*Keratella cochlearis* Gosse.
Brachionus budapestiensis Daday.	*Keratella quadrata* Müll.
Brachionus diversicornis Daday.	*Lecane (Monostyla) luna* Müll.
Brachionus quadridentatus Herm.	*Notholca squamula* Müll.
Conochilus unicornis Rouss.	*Microcodon claus* Ehrbg.
Filinia longiseta Ehren.	*Platyas quadricornis* Ehrbg.
Kellicottia longispina Kell.	

The accumulation coefficients of the investigated elements in the zooplankton varied from 10^2 to 10^7 (Figure 10). Such a high accumulative capacity of zooplankton compared to other hydrobionts (Timofeyeva-Resovskaya, 1963) shows its great value in self-purification of natural waters. The obtained data can be used to develop methods for indication of chemical pollution of continental reservoirs by plankton organisms (Leonova et al., 2006; Trapeznikov et al., 2008; Guseva and Chebotina, 2011). Moreover, the observed high affinity of omnipresent zooplankton species to certain trace elements in the water media allows one to consider the use of this biotic element in decontamination technologies (Polyakov and Egorov, 2003; Khlebnikov et al., 2011).

CONCLUSION

The results of a 25 year investigation on the state of the zooplankton complex in the cooling reservoir of the Beloyarskaya Nuclear Power Station revealed 31 species, among which 13 were cladocerans, 5 copepods and 13 rotifers. Generally, the group of crustaceans predominated in abundance and biomass, with cladocerans accounted for the largest percentage of the zooplankton biomass (75–85 %). The numerically most important crustacean species were *Bosmina kessleri*, *Chydorus sphaericus*, *Daphnia cristata*, *D. pulex* and *Eudiaptomus graciloides*. Abundance and biomass of the dominant species during the study period were highly variable and depended on many factors, including the season, temperature of the water medium, the sampling site, etc.

In the area adjacent to the nuclear power station (Teplyi Bay, water discharge and the SWD channels) the suppression of zooplankton was evident, and resulted to lower abundance and biomass, as well as to high mortality of organisms. The zooplankton abundance was almost four times lower in the heated water discharge zone compared to the control area, while its biomass was 7 times lower. The number of the younger specimens was also markedly lower. The results after various years of observation showed that there was significant zooplankton mortality after its passing along with water through the cooling system of the nuclear power station. In particular, the total abundance and biomass of zooplankton decreased approximately 3 and 2 times, respectively. Furthermore, the analysis of mortality of the dominant species indicated that copepods were more exposed to mechanical injury during passage through the cooling system than cladocerans. The effect of the SWD channel was manifested in the lower abundance and biomass of zooplankton (2 and 5 times, accordingly), compared with the control area, while the total number of species was two times lower and there was alteration in species dominance.

Finally, in the SWD channel, the average concentration of ^{90}Sr and ^{37}Cs in the zooplankton was 139 ± 17 and 3250 ± 250 Bq/kg, respectively, while in the upstream part of the reservoir being free of radionuclides, the respective concentrations were 5 and 7 Bq/kg. Compared with other hydrobionts and the sediment, phyto- and zooplankton had considerably higher accumulation coefficients. The accumulation coefficients of 70 chemical elements in the zooplankton ranged from 10^2 to 10^7. A significant positive correlation between concentrations of chemical elements in the zooplankton and in the water media indicated that zooplankton generally reflected the chemical composition of the environment.

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Chapter 6

SOME ASPECTS OF ZOOPLANKTON (CLADOCERA, COPEPODA) SPATIO-TEMPORAL DYNAMICS IN A LARGE RIVER: THE CASE STUDY OF THE DANUBE RIVER

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ABSTRACT

Despite rapidly growing insights into zooplankton spatio-temporal dynamics in lotic environments, syntheses of prior case studies have not yet been given much effort. We aimed to assemble the pieces of some of our previous case studies performed in the Danube River and to put all those findings into a more coherent framework. These studies do not cover the full range of dimensions affecting microcrustacean dynamics and diversity in the river, rather demonstrate a representative subset of spatio-temporal aspects of microcrustacean dynamics. We discuss the horizontal variation of crustacean zooplankton abundance across the river channel and demonstrate that different taxonomic and life-history clusters exhibit various patterns. The complex interactive effects of the flow regime with nutrient inputs on riverine zooplankton are discussed on the

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example of the waste water discharges entering the river at Budapest. We demonstrate the short-term variation of microcrustacean dynamics on the basis of samples collected on a daily basis. This sampling design allowed for testing the effects of sampling effort and sampling frequency on the estimation of the composition and abundance of microcrustacean assemblages in a side arm of the river. We discuss the possible effects of climate change on microcrustacean dynamics by means of a simple simulation model. Finally, a list of recommendations is given as how to improve our understanding in this evergreen field of limnology.

INTRODUCTION

The high level of spatio-temporal heterogeneity represents a unique feature of lotic ecosystems, which is best captured in the conceptual model of Ward (1989). This model assumes that the dynamic and hierarchical nature of lotic ecosystems can be studied along four dimensions. A couple of models have paved the road for a more thorough understanding of those dimensions, which have shaped our thinking about the structure and function of running waters and also have contributed to a better understanding of riverine plankton dynamics. The River Continuum Concept (Vannote et al., 1980) assumes that physical variables present a continuous gradient within a river system, producers and consumers are in harmony with dynamic physical conditions. Downstream communities utilize upstream processing leakage, community structure is predictable. The Serial Discontinuity Concept (Ward and Stanford, 1983) was adopted to rivers with impoundments, where the longitudinal resource gradient is intermitted along the river. Those impoundments shift abiotic and biotic patterns and processes, the magnitude and direction of which depend on the location of the impoundment. An extension of this model (Ward and Stanford, 1995) considers the lateral connection between the river channel and the floodplain, and defines the floodplain as an integrant component of the river system. The Flood Pulse Concept (Junk et al., 1989) goes beyond the spatial dimension and stresses the importance of periodic flooding, while the Riverine Productivity Model (Thorp and Delong, 1994) picks up local autochtonous production and organic matter of the floodplain. The retention capacity of the inshore (storage) zone has been proposed to be the major determinant of biological processes and biodiversity in large rivers (Inshore Retention Concept - Schiemer et al., 2001).

In this chapter, we will delve into some of those dimensions from the perspective of microcrustaceans. In order to understand zooplankton spatio-temporal dynamics in running waters, it is necessary to have a look at the origin and fate of their populations. Despite the ability of some species to face the current (Richardson, 1992; Jack et al., 2006), zooplankton organisms are generally assumed to be transported downstream and cannot build up significant populations in the main channel simply because of their relatively high generation time and physical damage by the flow (Hynes, 1970; Basu and Pick, 1996). At high water residence time, however, zooplankton (particularly rotifers and cladocerans) may develop significant populations in the main channel as well (Viroux, 2002; Wahl et al., 2008). Potamoplankton populations may develop only in rivers with a minimum length of 500-600 km assuming that the river receives no allochtonous input of zooplankton. The Danube River has an average water residence time of 26 days, allowing the development of 4-9 rotifer generations, 1-2 cladoceran generations and 1 copepod generation in transit (Naidenow, 1998). Reckendorfer et al. (1999) reason that *in situ* production of zooplankton in the Danube River (Austria) is of minor importance, because abundance of zooplankton reached the lowest values in low water in summer and this is in sharp contrast with that of discussed above. Assuming zooplankton flushing from lentic habitats, we expect individual numbers to increase with discharge. Reckendorfer et al. (1999) found the greatest number of inshore storage zones for zooplankton at intermediate water levels. The physical interaction between the flow regime and riverbank morphology determines the availability of inshore storage zones, so thus, it also determines the allochtonous plankton input. This retention capacity governs ecological processes and biodiversity in large regulated rivers (Schiemer et al., 2001). The lentic origin of zooplankton has received considerable support worldwide (e.g. Saunders and Lewis, 1988; 1989; Naidenow, 1998; Reckendorfer et al., 1999; Schiemer et al., 2001; Viroux, 2002), but additional factors such as *in situ* production and resting stages may contribute to potamoplankton dynamics as well (Wahl et al., 2008).

Abiotic factors may contribute to riverine ecosystem dynamics much more than do biotic factors (Lair, 2006). Because zooplankters arrive by chance in any habitat during dispersion, riverine plankton communities are primarily governed by non-predictable hydrodynamic conditions, water residence time and availability of habitats (Lair, 2006). Zooplankton abundance and species number increase with increasing distance from the main channel towards backwaters in line with increasing habitat heterogeneity and water residence time (a nice model presented in Paggi and Paggi (2007)). Communities in different habitats within the river system enter different states at low water due to local drivers, but flooding increases the similarity within habitats as regards physical, chemical and biological variables (Thomaz et al., 2007).

Generally, microcrustaceans play a secondary role in rivers as compared to rotifers, which is connected to the shorter generation time of rotifers (Lair, 2006). In addition, rotifers are supposed to benefit indirectly from river turbidity because their crustacean competitors and predators are relatively more susceptible to suspended sediments (Thorp and Mantovani, 2005). Riverine crustacean communities are often dominated by small-bodied cladocerans (e.g. bosminids) and juvenile forms (copepodite, nauplii) of copepods (Pourriot et al., 1997; Kobayashi et al., 1998; Reckendorfer et al., 1999; Kim and Joo, 2000; Vadadi-Fülöp et al., 2009).

Despite increasingly accumulating insights into zooplankton spatio-temporal dynamics in running waters, we will clearly benefit from a coherent view and rethinking of individual studies. We aimed to assemble the pieces of some of our previous case studies performed in the Danube River near Budapest and to put all those findings into a more coherent framework. Also we have updated some of our previously published data wherever indicated in the text later on this chapter. This chapter does not cover the full range of dimensions (i.e. horizontal - discussed in full; vertical - not discussed; longitudinal - partly discussed; temporal - discussed in full) affecting microcrustacean dynamics and diversity in the river, rather demonstrate a representative subset of spatio-temporal aspects of microcrustacean dynamics. The methods of sample taking and processing are discussed in Vadadi-Fülöp (2009; 2013), Vadadi-Fülöp et al. (2009; 2010).

THE DANUBE RIVER

The Danube River is the second largest river in Europe with a catchment area of 817,000 km^2. The catchment covers 19 countries making the river the most international one in the world, and thus giving rise to a growing demand for the protection of its water quality. The flow regime of the middle reach is largely determined by the upper reaches of the river. The Budapest section lies within the middle reach and receives a discharge of approximately 500-600 m^3 s^{-1} at low water and 6,000-8,000 m^3 s^{-1} at high water (Berczik, 1965). Much of the shoreline is regulated with a mosaic of rip-rap and gravel.

The river experiences algal blooms even in winter (Kiss and Genkal, 1993) and undergoes marked eutrophication (Kiss, 1994). Nutrients do not limit algal growth, instead the flow regime and light (i.e. thickness of the euphotic zone) determine phytoplankton development in the Danube (Kiss, 1994; Vörös et al., 2000). The growing number of impoundments and subsequent decrease in suspended matter resulted in an increase of phytoplankton biomass in the 1970-80s (Kiss, 1994) with a parallel increase in zooplankton abundance (Bothár, 1988). Evidence derived from long-term analysis of phytoplankton in Hungary, however, indicates an increase in phytoplankton diversity and a decrease in biomass over the period of 1979-2002 (Verasztó et al., 2010). The abundance of microcrustaceans also declined in the 1990s (Bothár, 1994).

HORIZONTAL DISTRIBUTION OF MICROCRUSTACEANS ACROSS THE RIVER CHANNEL

The resampling bootstrap method (Efron, 1979; Efron and Tibshirani, 1993) was used to estimate the sampling distribution, since no replicate samples were taken at a given site. A two sample t-test was used to test for significance among microcrustacean densities across the river channel near Budapest (Table 1). For a more detailed presentation of methods see Vadadi-Fülöp et al. (2009), note however, that results presented here are an extension of what have been published in Vadadi-Fülöp et al. (2009). Densities of cladocerans, adult copepods, copepodite stages, nauplii, *Thermocyclops crassus*, *Moina micrura* and *Bosmina longirostris* were considered. Results indicate that densities of adult copepods, *T. crassus*, *M. micrura* and *B. longirostris* varied significantly between the left and right riverbanks. Densities of cladocerans, nauplii, *M. micrura* and *T. crassus* were lower in the middle of the river channel than in the right bank, while densities of adult copepods, nauplii, cladocerans, *T. crassus* and *B. longirostris* varied between the left bank and the middle of the channel, again with lower densities in the latter.

The bootstrap samples were analysed with the NMDS method (non-metric multidimensional scaling) allowing for a visual representation and a support of previously established findings. Each pairwise comparison resulted in a significant separation on the NMDS plot thus supporting spatial variation of densities across the river channel (Figure 1). The above presented findings thus support the significance of the horizontal dimension. Some prior studies also have pointed out that zooplankton may exhibit both vertical and horizontal patchiness in the river channel, particularly at low water (Marneffe et al., 1996; Viroux, 1999; Jack et al., 2006; Casper and Thorp, 2007).

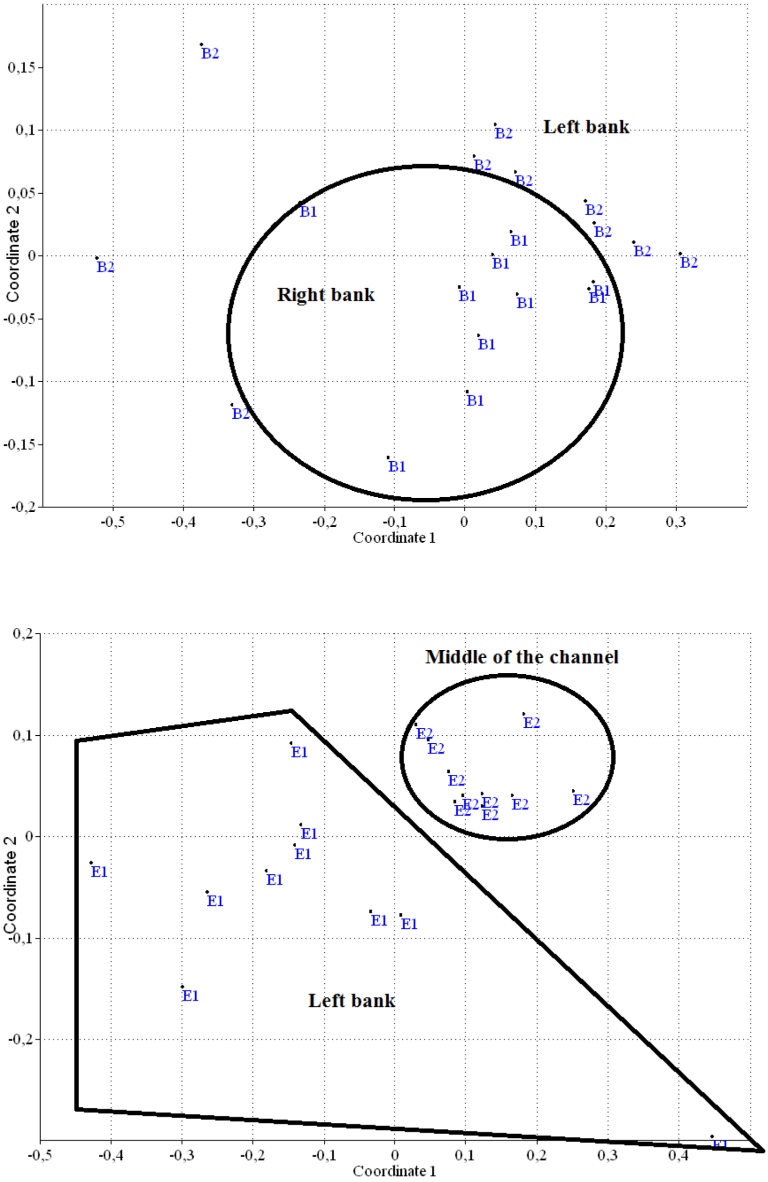

Figure 1. (Continued).

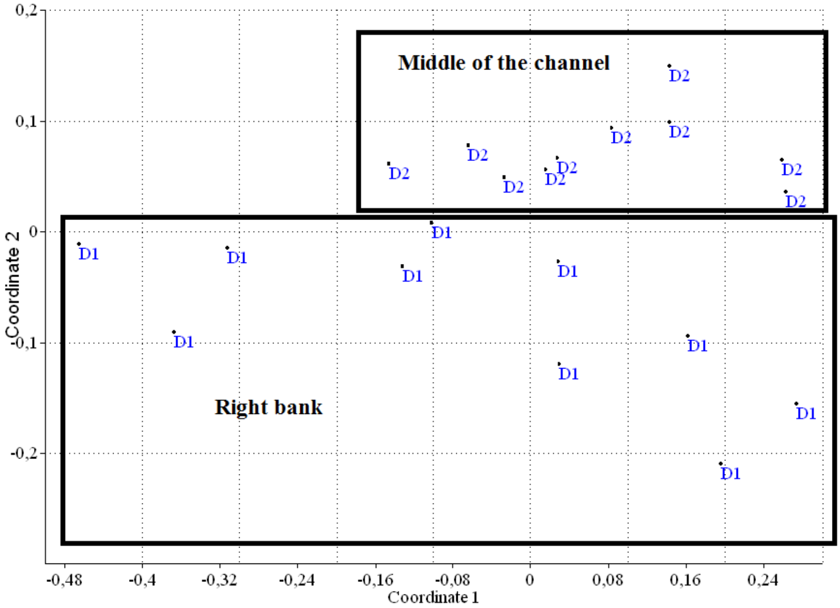

Figure 1. Comparison of microcrustacean densities across the river channel (NMDS plots) - Stress values 0.050; 0.047 and 0.072, respectively.

Table 1. Comparison of microcrustacean densities across the river channel (two sample t- test)

Taxa	Right bank vs. left bank	Right bank vs. middle of the channel	Left bank vs. middle of the channel
Adult copepods	-3.254**	0.331	5.423***
Copepodites	-1.931	0.873	2.069
Nauplii	0.077	-2.171*	3.252**
Cladocerans	-1.240	4.104**	5.917***
Moina micrura	-3.446**	3.403**	-0.129
Thermocyclops crassus	-2.697*	4.013***	3.096**
Bosmina longirostris	-3.440**	-0.830	4.728***

Significance levels: *$p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Effect of Sampling Effort on the Estimation of the Composition of Microcrustacean Assemblages

By means of samples collected on a daily basis (through 39 days), the short-term variation of microcrustacean dynamics was demonstrated in Vadadi-Fülöp et al. (2010). This sampling design allowed for testing the effects of sampling effort and sampling frequency on the estimation of the composition and abundance of microcrustacean assemblages in a side arm of the river. In the field, we collected individual samples of 50 litres. A total of 1,950 litres (50 X 39) of water was sampled during the 39-day sampling period. Suppose we collect samples at two-day intervals, we can do this in two ways depending on the first sampling date. It means 1,000 and 950 litres of water, respectively, depending on the sum of samples (20 and 19 samples, respectively). At three-day intervals there are three possible outcomes, finally when we take only one sample within the 39-day period, there are 39 possible samples each containing 50 litres of water. Thus, a total of 780 samples can be generated. Since it is a short period the results are not affected by seasonal dynamics and the individual samples can be summed. When we plot the sample size (volume of water) against the number of taxa, it will form an accumulation curve (Vadadi-Fülöp et al., 2010). The results suggest that a 50-litre water sample does not permit of detecting several taxa. At least 200 litres of water should be filtered through the plankton net in order to detect some half of the species, however, 1,000 litres would be ideal (when the accumulation curve gets saturated) for detecting the majority of species (about 90%). From another point of view, sampling 1,000 litres of water is the equivalent of a 20-day sampling period. If we measure the sample size at a logarithmic scale the relationship between sampling size and the number of taxa can be described by a linear regression (Figure 2).

The effect of sampling effort (i.e. sample size) was also analysed with a sophisticated method of early plant coenology (Du Rietz et al., 1920). We plotted the five constancy levels of species (0-20, 21-40, 41-60, 61-80, 81-100%) against the number of species (Figure 3). Theoretically, when the sample size has reached the constant minimal area of the community the curve turns into U-shape meaning that the relative contribution of the constant and accidental species increases while the number of accessory species remains low. The curve will become asymmetrical with the highest values at lower constancy levels when the constant minimal area is not reached, as the number of absolute constant species remains low.

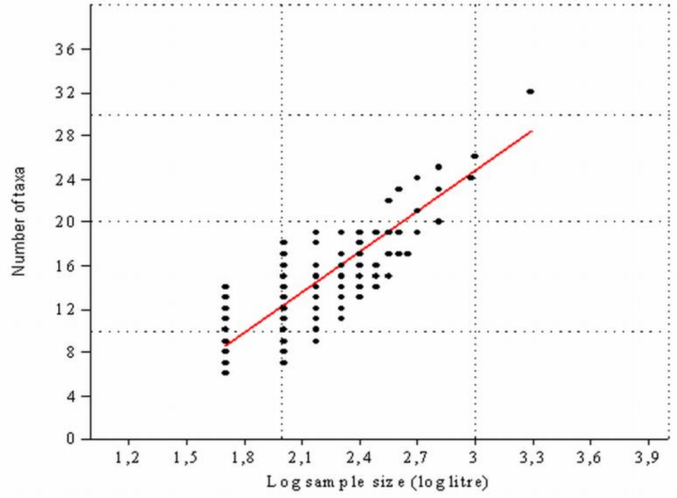

Figure 2. Relationship between log sample size and number of taxa. Regression equation: Number of taxa = -12.36 + 12.458 log sample size. Standard error for the slope: 0.26; standard error for the intercept: 0.49; $R^2 = 0.82$; $N = 780$; $p < 0.001$.

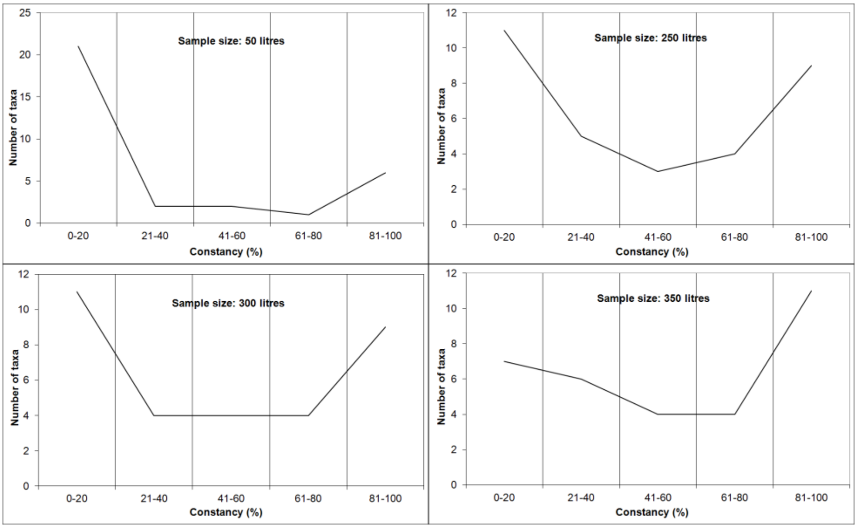

Figure 3. Relationship between constancy levels and number of taxa in case of 50, 250, 300 and 350 l of water as sample size (Du Rietz curves).

Similarly, after going beyond the constant minimal area, the number of constant species may increase notably, resulting in asymmetrical curve with maximum values at higher degree of constancy. Results suggest that sampling some 300 litres of water is sufficient for achieving the constant minimal area (i.e. minimal sample size) of microcrustaceans in the side arm of the river. 50 litres of water does not represent the constant minimal area as the number of constant species remains low whereas accidental species hit larger values. Sampling 350 litres of water will lead to an asymmetrical curve with a large number of constant species indicating that the constant minimal area has been overestimated.

According to the methods discussed above, the minimal sample size resulted in 1,000 and 300 litres of water, respectively. This sampling effort is beyond the sample size employed in potamoplankton studies: 10 litres (Illyová, 2006), 20 litres (De Ruyter van Steveninck et al., 1990), 25 litres (Vranovsky, 1991), 30 litres (Saunders and Lewis, 1989), 40 litres (Reckendorfer et al., 1999), 50 litres (Gulyás, 1995), 60 litres (Ietswaart et al,. 1999), 100 litres (Gulyás, 1994; Zarfdjian et al., 2000), 200 litres (Bothár, 1988; Bothár and Kiss, 1990; V.-Balogh et al., 1994). Obviously taking 1,000 litres of water would mean an enormous effort and sampling such a large volume of water will represent about 90% of the species in one sample. Also, the size of minimal area is subject to seasonal and regional variations (Kronberg, 1987). The results are based on a 39-day period which is not capable of detecting seasonal patterns while the seasonal changes in zooplankton species composition are well-documented in rivers as well (Tubbing et al., 1994; Kobayashi et al., 1998, Kim and Joo, 2000; Zarfdjian et al., 2000; Illyová, 2006). Considering the limitations discussed above, results should be handled carefully before extrapolation either in a spatial or temporal point of view.

EFFECT OF SAMPLING FREQUENCY ON THE ESTIMATION OF THE COMPOSITION AND ABUNDANCE OF MICROCRUSTACEAN ASSEMBLAGES

A single index (Potential Dynamic Information loss; PDI) was introduced to determine the loss of information in % (i.e. loss in the estimation of diversity, abundance etc.) when sampling frequency is reduced (Vadadi-Fülöp et al., 2010). This index can be calculated as follows. Take the variation of an arbitrarily selected variable (e.g. abundance) within a given sampling interval (e.g. within a two-day interval) and divide this number by the variation within the entire sampling period and then multiply the quotient by 100.

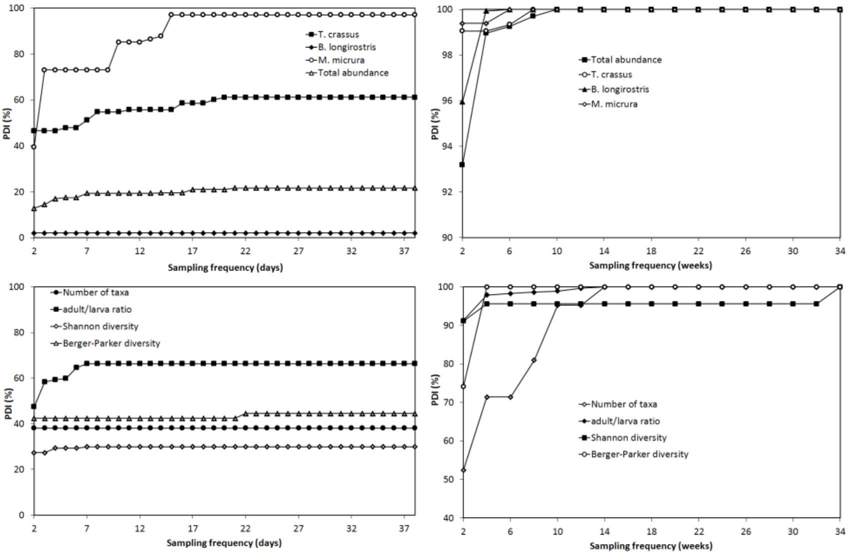

Figure 4. Potential Dynamic Information (PDI) loss of community attributes at different sampling frequencies.

The PDI index was calculated for the total abundance of microcrustaceans, number of taxa, densities of *Thermocyclops crassus, Bosmina longirostris* and *Moina micrura*, as well as for the adult/larva ratio of copepods, and for the Shannon and Berger-Parker indices. The loss of information refers to the loss in the estimation of the above-mentioned variables when sampling ferquency is reduced. The findings presented here, are an extension of what have been published in Vadadi-Fülöp et al. (2010), because we expanded the sampling period by half a year and thus the PDI indices have been updated. Figure 4 presents the PDI index at daily sampling frequencies (based on the calculations for the 39-day period in June-July 2007), as well as the information loss at biweekly sampling frequencies (based on the calculations for the entire, two-year long - October 2006-October 2008 - study period excluding samples taken on the daily basis). Results suggest that there are large differences in the estimation of densities of different species, namely *T. crassus* densities changed rapidly whereas *B. longirostris* densities varied slightly within the 39 day-period. It means that the individual numbers of *T. crassus* experienced large fluctuations in the 39-day term when compared to the variation within the entire study period. As a consequence, the estimation of this variable carries 47% loss of information when samples are taken at a two-day frequency. However, looking at the entire sampling period, *B. longirostris* densities showed large variation within 2 weeks (95%), which is due to the fact, that the abundance peak was not observed within the period of daily sampling, but in May 2008. Thus, it appears that the PDI index indicates minor variation at a daily frequency when compared with the entire study period. Similarly, the adult/larva ratio of copepods implied larger fluctuations within the 39-day term, but it is less true for the Shannon diversity. All variables displayed major variation (above 50%) within two weeks. The variation in the number of taxa was constant (38%) over the 39-day period and reached the 100% limit at a 14-week sampling frequency. Total zooplankton abundance varied moderately within the 39-day period, but showed major variation (93%) within two weeks considering the entire study period, owing to the peak density of *B. longirostris*.

Generally, seasonal dynamics of riverine zooplankton has been discussed on the basis of samples collected at biweekly (Reckendorfer et al., 1999; Kim and Joo, 2000; Zarfdjian et al., 2000) or weekly intervals (Bothár, 1988; Bothár and Kiss, 1990; V.-Balogh et al., 1994). Bothár (1996) performed zooplankton investigations on daily basis in the Danube River and pointed out that no regular quantitative change or fluctuation in zooplankton abundance can be observed although phytoplankton and water chemical data showed regular daily patterns. Copepods showed 2-3-day periodicities, which the author attributed to the structural changes of different developmental stages. The author considered the weekly sampling strategy as an adequate tool to get a clear picture of the species composition and quantitative changes of zooplankton in the river. Results presented in this chapter although derived from a side arm of the Danube River indicate that abundances may experience notable variation even within a week, so do diversities and adult/larva ratios. According to the findings of a two-year long study period, samples taken at biweekly frequencies may not be always sufficient to track microcrustacean seasonal dynamics (PDI for total abundance reached 93% within two weeks). This is partly due to the relatively short generation time of cladocerans. Present chapter is only confined to planktonic crustaceans, however, rotifers are characterized with shorter generation times (Lair, 2006) and they are often the dominant component of riverine zooplankton (Gulyás, 1995 - Danube River; Burger et al., 2002 - Waikato River; Kim and Joo, 2000 - Nakdong River; Zarfdjian et al., 2000 - Aliakmon River; Saunders and Lewis, 1988 - Apure River; Saunders and Lewis, 1989 – Orinoco River; Dijk and Zanten, 1995 - Rhine River; Thorp et al., 1994 - Ohio River). Hence additional studies on a broad range of taxa is clearly needed in this aspect.

EFFECTS OF THE FLOW REGIME ON MICROCRUSTACEAN DYNAMICS AND DIVERSITY

To answer the question of whether there is any variation in microcrustacean densities and diversities in either side of Budapest (with its considerable waste water inflows), samples of crustacean plankton were taken over a period of 26 months just upstream and downstream of Budapest (Vadadi-Fülöp, 2013). The flow regime can mask the effect of waste water discharges by diluting the concentration of nutrients and pollutants, therefore we put forward the hypotheses that as a result of waste waters (i) microcrustacean abundance will increase downstream, (ii) diversity and species richness will decrease downstream, and (iii) this variation is related to the flow regime and can be detected under periods of low flow only.

Although all the samples taken from the midchannel and river banks were counted individually, they were pooled for statistical analyses in order to derive better estimates of densities per upstream ($N = 48$) vs. downstream sites ($N = 48$). According to the hypotheses and preliminary results, the data set was first divided into low water (discharge < 1,920 $m^3 s^{-1}$; $N = 24$) and high water (discharge > = 1,920 $m^3 s^{-1}$; $N = 24$) periods, respectively, both for upstream and downstream sites. This partition corresponds to the long-term average discharge recorded at Budapest (2,200 $m^3 s^{-1}$) and allows N to be equal among ’treatments’. The resampling bootstrap method (Efron, 1979; Efron and Tibshirani, 1993) was used to estimate the sampling distribution, since no replicate samples were taken at the same site. We generated 10 bootstrap samples per sampling site at low water and high water periods, respectively. The bootstrap samples allowed testing for significance among upstream and downstream reaches, as well as among different hydrological phases using a parametric two sample t-test.

Densities showed quite similar patterns among upstream and downstream sites with peak densities of similar timing, magnitude and duration (Vadadi-Fülöp, 2013). Densities recorded upstream during high water were comparable to those recorded downstream, densities at low water, however, increased considerably downstream. The juvenile stages of copepods and particularly the population of *Thermocyclops crassus* may account for this increase. In contrast, the cladoceran *Moina micrura* reached relatively high densities upstream at low water. The two sample t-test allowed testing for significance among upstream and downstream reaches, as well as among different hydrological phases (Table 2). Copepodite ($p < 0.01$) and adult copepod ($p < 0.001$) densities varied significantly among upstream and downstream sections at low water (downstream increase), but differences in nauplii and cladoceran densities did not reach the significance level. In contrast, densities of nauplii ($p < 0.05$) and adult copepods ($p < 0.001$) differed significantly among upstream and downstream reaches at high water, i.e. nauplii decreased while adult copepodes increased in densities downstream. Out of 8 possible comparisons within sections, 5 were significantly different, when densities of different taxonomic and life-history clusters were contrasted among different hydrological phases (Table 2). High water was coupled with increased densities both upstream and downstream.

Table 2. Comparison of microcrustacean densities among upstream and downstream sites as well as among different hydrological phases (two sample t-test)

Taxa	Upstream vs. downstream		High water vs. low water	
	Low water	High water	Upstream	Downstream
Adult copepods	-8.363***	-4.104***	-6.227***	0.331
Copepodites	-3.711**	0.006[a]	-3.442**	-1.572
Nauplii	-0.152	2.515*	-8.071***	-2.705*
Cladocerans	2.005	-1.627	-1.480	-3.737**

Significance levels: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

[a] derived from Welch test.

The Shannon diversity of microcrustacean assemblages peaked at high water both upstream and downstream of Budapest, with marked longitudinal variation at low water. The number of taxa exhibited similar patterns. The relative abundance of tychoplanktonic species increased at high water, particularly upstream of Budapest, which resulted in a marked difference among upstream and downstream reaches at high water. Relative abundances of the euplanktonic *Moina micrura* and *Thermocyclops crassus* decreased considerably with rising water level both upstream and downstream. The Berger-Parker index decreased markedly at high water both upstream and downstream indicating greater evenness when the water level rises (Figure 5). Comparison between sections indicated a marked difference between upstream vs. downstream reaches at low water with greater dominance at the upstream site. The relative abundance of egg-carrying individuals did not vary between hydrological phases, but increased downstream considerably. This downstream increase reflects longitudinal variation in copepod densities.

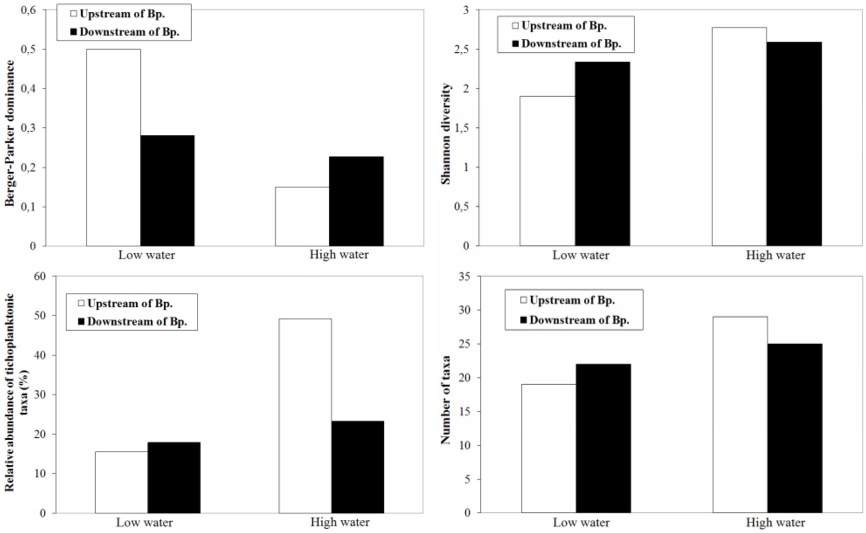

Figure 5. Longitudinal variation in different community attributes at different hydrological phases.

We contrasted diversities using the Shannon diversity t-test, which revealed statistically significant differences among upstream and downstream sections at low water (t = -3.133; $p < 0.01$) but not at high water (t = 1.649; p = 0.099). The Berger-Parker dominance may explain this variation: the upstream site is more strongly dominated by the prevailing species (*Moina micrura*) than the river stretch downstream of higher evenness. Moreover, three additional species were recorded downstream at low water. Diversities also varied significantly among different hydrological phases both upstream (t = -6.235; $p < 0.001$) and downstream of Budapest (t = -2.512; $p < 0.05$).

In summary, results indicated that both densities and diversities of microcrustaceans vary significantly among upstream and downstream sites, as well as among different hydrological phases. Similarly to the papers of Sabri et al. (1993), Onwudinjo and Egborge (1994), Reckendorfer et al. (1999), and Wahl et al. (2008), high water was coupled with increased densities and diversities of microcrustaceans both upstream and downstream, suggesting importance of downstream transport from source areas. Peak densities, however, did not correspond to peak discharges, but instead corresponded to moderately high water levels, thereby supporting the Inshore Retention Concept of regulated large rivers (Schiemer et al., 2001). This is in contrast to evidence derived from some tropical rivers (Saunders and Lewis, 1988; Saunders and Lewis, 1989; Frutos et al., 2006) despite a similar importance of washout effects. One possible explanation is that those rivers are rather unregulated and have a more predictable flow regime due to the alteration of wet and dry seasons than do temperate rivers, such as the Danube. The findings, however, are in contrast with that of Pace et al. (1992), Thorp et al. (1994), Gulyás (1994), Basu and Pick (1996). On the basis of the above-mentioned discussion, we propose that local factors and even the sampling frequency and the data analyses used may substantially modify final conclusions. One would argue that division of data into low water and high water categories may lead to false conclusions given that the low water period is strongly coupled with autumn and winter months when microcrustaceans decrease in density irrespectively of the flow regime. This argument does not apply to this chapter, the flow regime varied both within and among seasons with marked discharge peaks in autumn as well. High and low water periods, as defined in this chapter, are independent of water temperatures and season and therefore represent a ’superior’ driving force.

Several case studies have documented the negative effects of waste waters on potamoplankton (Naidenow and Saiz, 1985 - Danube River; Marneffe et al., 1996 - Meuse River; Olguin et al., 2004 - Reconquista River; Gagneten and Paggi, 2009 - Salado River), while others have not found evidence for such coupling (Kalafatic, 1984 - Danube River; Bonecker et al., 1996 - Doce River). In the Hungarian section of the Danube, effects of waste water discharges were found to be subject to the water level with declining number of taxa under periods of low flow (Gulyás, 1994). Gulyás (1997) did not find marked difference in densities of zooplankton among samples taken just upstream and downstream of Budapest. We demonstrated significant differences among upstream and downstream sites in terms of densities and diversities particularly at low water. Further analyses indicate, however, that taxonomic and life-history clusters exhibit different responses. Diversities did not experience a decline downstream, the flow regime seems to be masking any effects of waste water discharges.

Although diversities declined with decreasing water level, it seems to be the result of decreasing plankton input from source areas (i.e. decreasing number of tychoplanktonic species and parallel increase in dominance of euplanktonic species) rather than the sign of deterioration in water quality. Similarly, we suggest that the flow regime explains longitudinal variation in community structure and densities, rather than water quality. All those findings point towards a significant dilution effect. We argue that effects of waste waters are embedded within the river flow effect in such a way that, the latter appears to mask the impact of industrial and municipal discharges. This chapter of the Danube River supports earlier findings that the flow regime maintains biodiversity in floodplain rivers (Poff et al., 1997).

PROJECTED SEASONAL DYNAMICS OF *CYCLOPS VICINUS* – POSSIBLE SCENARIOS

Quantitative data on copepods and cladocerans are available for the period of 1981-1994 (except the year 1990) based on the database of the Hungarian Danube Research Station of the Hungarian Academy of Sciences. Surface samples near to the riverbank were collected in the main arm of the Danube River at Göd (1,668 rkm), filtering 200 litres of water through a plankton net of 75μm mesh size. The weekly sampling design allowed to develop a simulation model of *Cyclops vicinus* abundance, considering some meteorological variables as input data provided by the Hungarian Meteorological Office (Sipkay et al., 2008). Three data series of daily temperatures projected for the period of 2070-2100 were used, which are based on the A2 and B2 scenarios recommended by the IPCC (Solomon et al., 2007). We adopted the database of the PRUDENCE EU project (Christensen, 2005), namely the A2 and B2 scenarios of the HadCM3 climate change model developed by the Hadley Centre (HC). Furthermore, the A2 scenario of the Max Planck Institute (MPI) was used. Daily data projected to the period of 2070-2100 (31 years) were downscaled to the region of Budapest.

The model assumes that temperature is the driving force of plankton dynamics, so thus the abundance pattern is determined by the minimum and maximum temperatures (and also by the abundance of the population on the preceding day), other factors (e.g. trophic interactions) may appear as hidden or as integrated into the main effect. We suppose that the temperature reaction-curve of *Cyclops vicinus* is the sum of optimum curves, since the temperature optimum-curves of different developmental stages of *Cyclops vicinus* or its distinct subpopulations can be combined into the reaction-curve. The seasonal dynamics of copepodites and adults were simulated as described in Sipkay et al. (2008). The model was launched with the daily data series of climate change scenarios discussed above, starting each year with an initial copepodite and adult abundance. The onset of peak abundance was used as indicator, one-way ANOVA was used to test whether there is any significant difference in *Cyclops vicinus* phenology among scenarios. The post-hoc Tukey-test was performed to test for significant differences between groups in pairwise comparisons. Abundance peaks of *Cyclops vicinus* did not vary significantly among scenarios ($p = 0.07$; ANOVA). Results suggest that A2 and B2 scenarios of the Hadley Centre are more similar compared to the output derived from the A2 scenarios of the MPI and that of the Hadley Centre.

In the model fitted to the observed data (between the years 1981 and 1994), peak abundance appeared between Julian days 111 and 153, on the average on Julian day 137 (17th May). In contrast, *Cyclops vicinus* is projected to reach peak abundance 1-1.5 months earlier; i.e. on the average on Julian day 93 (A2, MPI), 98 (B2, HC) or 101 (A2, HC), consequently between the 3rd and 11th April.

Table 3. Observed and simulated timing of peak abundances of *Cyclops vicinus* as well as the annual and peak abundances measured between 1981-1994 and projected to 2070-2100

Onset of the peak (Julian day)	Observed data (%)	A2 (HC) (%)	A2 (MPI) (%)	B2 (HC) (%)
<100	0	42	65	45
101-130	30	55	29	55
131-160	70	3	6	0
>160	0	0	0	0
Peak abundance (ind. m^{-3})	Observed data (%)	A2 (HC) (%)	A2 (MPI) (%)	B2 (HC) (%)
<100	20	39	16	45
101-400	50	23	10	13
401-800	30	3	3	6
>800	0	35	71	36
Annual abundance (ind. m^{-3})	Observed data (%)	A2 (HC) (%)	A2 (MPI) (%)	B2 (HC) (%)
<3.000	20	55	19	45
3.001-6.000	40	13	6	10
6.001-20.000	40	6	7	19
>20.000	0	26	68	26

Peak abundances and annual abundances are projected to experience large fluctuations (Table 3). Scenarios forecast lower or markedly higher peak abundances and annual abundances as compared to the reference period of 1981-1994. Only the A2 scenario of the Max Planck Institute indicates that abundances will shift towards higher values definitely. The results however should be handled carefully owing to the very simple (yet validated) model and also because the scenarios are outcomes of different climate models which carry another point of uncertainty.

CONCLUSION

We can conclude that findings may, in a surprisingly significant extent, be subject to the selected sampling strategy. Fully aware of the limitations of such individual case studies, results on a side arm of the Danube River indicate that densities may experience significant variation even within a week as do diversities and adult/larva ratios. A biweekly sampling design adopted by the majority of riverine plankton studies may be even subject to a ~90% error in the estimation of densities and diversities, as short generation times of microcrustaceans allow rapid development in a relatively short timeframe under favourable conditions. This is more evident for the rapidly expanding populations of rotifers and algae. The timing of abundance peaks depends on a large number of environmental variables and trophic interactions, and can be even subject to the weather conditions of the preceding winter (Straile, 2000; Gerten and Adrian, 2000) although appears somewhat predictable in lakes (Sommer et al., 1986). A sample size of 200 litres would be needed to detect some half of the species in a definite sample, however, 1,000 litres would be ideal for detecting the majority of species, which is the equivalent of a 20-day sampling period. Again, considering the limitations of what we have discussed earlier in this chapter the findings clearly cannot be projected either to the main channel of the Danube River, or other large rivers, but the authors encourage colleagues interested in zooplankton seasonal dynamics to test for similar effects.

The horizontal dimension of plankton dynamics represents another important aspect of the sampling strategy. We did not find general patterns for microcrustacean distribution, different species and life-history clusters exhibited variable patterns across the river channel. Such horizontal patchiness along with vertical variation in distribution of zooplankton has been increasingly recognized in running waters (Marneffe et al., 1996; Viroux, 1999; Jack et al., 2006; Casper and Thorp, 2007).

The longitudinal dimension of running waters and plankton dynamics has only been marginally discussed in this chapter because the sampling design was not longitudinal in a true sense (i.e. the sampling stations upstream and downstream of Budapest lie within a distance of ~40 km), as we targeted the local effects of the waste water discharges rather than the longitudinal development of zooplankton assemblages. In Vadadi-Fülöp (2009) we failed to demonstrate significant relationship between the flow regime and microcrustacean densities downstream of Budapest and found only a weak although significant coupling between those upstream of Budapest. We argue that shortcomings of the correlative approach may account for those findings. Cutting edge papers often apply correlative approaches and regressions to reveal the relationship between the flow regime and zooplankton densities (Pace et al., 1992; Thorp et al., 1994; Basu and Pick, 1996; Baranyi et al., 2002; Rossetti et al., 2009). Empirical evidence derived from correlative approaches, however, appears to be constrained at least by three properties of the flow regime: (i) the availability of inshore storage zones of plankton appears to peak at intermediate water levels (Reckendorfer et al., 1999; Schiemer et al., 2001); (ii) the sum of *in situ* production (low water) and washout effects (high water) may account for variation in densities in rivers with high variations of flow and with an extended floodplain; (iii) flooding events are coupled with high concentrations of suspended sediments, hampering feeding in filter-feeders (Arruda et al., 1983; Hart, 1988), and thus counteract any washout effects. These effects may add a very large amount of background noise to the analysis. To address this issue, we divided the data into ’high water’ and ’low water’ periods irrespectively of the season and then contrasted microcrustacean densities and diversities considering the impact of waste water discharges entering the river at Budapest (Vadadi-Fülöp, 2013). In a nutshell, the statistical analysis employed to assess data, as practically anywhere in biology, can modify final conclusions.

Peak densities of microcrustaceans did not correspond to peak discharges, but instead corresponded to moderately high water levels. It thus appears that the Inshore Retention Concept of regulated large rivers proposed by Schiemer et al. (2001) can be a realistic model to assess zooplankton dynamics in the middle section of the Danube River. We found that effects of waste waters are embedded within the river flow effect in such a way that, the latter appears to mask the impact of industrial and municipal discharges. Fully aware of the limitations of such case studies, it means that the hydrological regime appears to be a superior driving force governing microcrustacean dynamics in the Danube River. Such findings do not imply, however, that waste waters are of minor importance, rather reflect the buffering capacities of running waters with high discharges.

Lakes and rivers (Williamson et al., 2008; Adrian et al., 2009; Schindler, 2009) as well as ongoing plankton monitoring programmes (Hays et al., 2005) have been recognized as sentinels of global change. Despite rapidly growing evidence for climate change-related variation in zooplankton phenology, abundance, distribution, body size, community structure, life-history and behaviour in lakes and the marine realm, our understanding of those phenomena in running waters is still very limited (for more details, see Vadadi-Fülöp et al. (2012)). The case study on *Cyclops vicinus* supports the clear need for a more thoroughly consideration of potamoplankton in climate change research.

Putting together the pieces of our case studies performed in the Danube River raises new questions: Out of the four dimensions of running waters (Ward, 1989) which can be regarded as the most important one? Clearly, the temporal and longitudinal dimensions have been targeted more frequently, while the vertical and horizontal dimensions have been partially overlooked yet. The authors encourage colleagues to conduct a large-scale study in equal consideration of the four dimensions and then decipher the contribution of dimensions one by one. Lotic ecology also may benefit from (i) a more thorough consideration of the horizontal dimension of lotic ecosystems; (ii) a more appropriate selection of sampling strategies possibly underpinned by preliminary field data (significance of the temporal dimension); (iii) using alternative approaches over correlations when discussing the relationship between the flow regime and zooplankton dynamics and (iv) paying more attention to climate change impacts on potamoplankton (long-term time scale).

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Chapter 7

ABUNDANCE AND TROPHIC POSITION OF GELATINOUS ZOOPLANKTON IN THE NAMIBIAN UPWELLING REGION

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ABSTRACT

Cnidaria and Ctenophora are carnivorous gelatinous organisms mainly feeding on zooplankton, fish larvae and small fishes and are considered as end members of the food web as they are only eaten by a few species like some fishes, other cnidarians and sea turtles. Since the 1970's the abundance of large gelatinous zooplankton increased in the

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northern Benguela probably due to overfishing and/or climate change. Although information on the abundance of large gelatinous organisms like *Chrysaora* spp. or *Aequorea* spp. exists, little is known about smaller-sized gelatinous organisms which can be caught with plankton nets. In this chapter, we will present data about the onshore/offshore and vertical distribution as well as the taxonomical composition of these organisms in the northern Benguela Current System. Furthermore, we will provide insights into their trophic position using a stable isotope analysis. Samples were taken with a multiple opening and closing net in March 2008 and in December 2009 along a transect off Walvis Bay (Namibia) from the shelf towards the open ocean. Additional samples were taken with different types of gears at several stations in the northern Benguela for stable carbon and nitrogen isotope analyses in December 2009. The taxonomical composition of all groups revealed an inshore/offshore gradient with higher diversity offshore. Medusae and Siphonophora were treated separately since Siphonophora live in colonies which break into pieces when caught by nets. Medusae were generally smaller in size at the offshore station, whereas no size distribution gradient was found for the single individuals of Siphonophora. The numerical abundance of both Medusae and Siphonophora parts were variable along the onshore-offshore transect. Within the Medusae, Trachymedusae dominated the offshore system and Leptomedusae the inshore system. Within the Siphonophora, the system was dominated by Diphyidae in offshore and costal waters and on the inner shelf in 2008 and by Agalmatidae at the slope, shelf-break, outer shelf and inner shelf in 2009. A heterotrophic level of two and higher was calculated for the gelatinous zooplankton.

Keywords: Gelatinous zooplankton, trophic position, stable isotopes, Namibian upwelling, Benguela

INTRODUCTION

The term "gelatinous zooplankton" is used in different ways. Some authors only include Coelenterata (Cnidaria and Ctenophora) into this term (Haddock, 2004), whereas others also include Salpidae, Chaetognatha and some Mollusca like Pteropoda (Harbison, 1992; Raskoff et al., 2003). In our study, "gelatinous zooplankton" consists of Coelenterata only. There is some evidence that the abundance and biomass of gelatinous zooplankton has heavily increased after the collapse of fish stocks in the 1970s in the Benguela Upwelling System (BUS); however, these animals are not randomly distributed and show distinct spatial and temporal patterns (Lynam et al., 2006; Utne-Palm et al., 2010; Flynn et al., 2012). The BUS extends along the west coast of South Africa, Namibia and Angola from 34°S to 17°S (Hart and Currie, 1960). The system is characterized by episodic upwelling events, which are driven by strong equatorward winds. Maximum upwelling occurs from April to December (Hutchings et al., 2006) with a peak between July and September (Hagen et al., 2001). A high abundance of large Medusae was not reported in the region during detailed plankton studies in the 1950s and 1960s (Hart and Currie, 1960; Stander and De Decker, 1969). The first note of high amounts of jellyfish in the BUS was during the beginning of the 1970s (King and O'Toole, 1973; Cram and Visser, 1973; Schülein, 1974). It is still uncertain whether this increase of jellyfish stocks in the region was caused by the overexploitation of fish (Pauly et al., 1998), global climate change (Mills, 2001; Purcell, 2005) or eutrophication (Arai, 2001). Flynn et al. (2012) concluded that jellyfish abundance increased with a decline of fish stocks in the northern BUS. However, this is not a unique BUS phenomenon; similar increases in gelatinous zooplankton were observed at a number of locations worldwide (Brotz et al., 2012): e.g., large Medusae in the Bering Sea (Mills, 2001), *Pelagia noctiluca* in the Mediterranean Sea (Mills, 2001), large Scyphozoa in the Yellow, Bohia and East China Seas (Dong et al., 2010), *Mnemiopsis leidyi* in the Black Sea (Mills, 2001) and Baltic Sea (Javidpour et al., 2009). Therefore, it is evident that management actions are necessary to deal with the increase in jellyfish abundance (see Richardson et al., 2009).

Although several papers about the taxonomy (Pagès and Gili, 1992; Pagès et al., 1992) and ecology (e.g. Buecher et al., 2001; Gibbons and Buecher, 2001; Buecher and Gibbons, 2003) of gelatinous zooplankton in the northern Benguela region exist, data on the vertical and horizontal distribution of small Medusae and their role in food web dynamics are still limited. Only the distributions of large jellyfish like *Chrysaora* spp. and *Aequorea* spp. were examined in several studies (e.g. Fearon et al., 1992; Brierley et al., 2001; Sparks et al., 2001; Flynn et al., 2012) as well as the effects of advective processes on gelatinous zooplankton (Pagès and Gili, 1991).

The position of gelatinous zooplankton within the food web of several ecosystems was determined by gut content analyses and observations (e.g. Fancett and Jenkins, 1988; Båmstedt and Martinussen, 2000; Flynn and Gibbons, 2007). Since the 1970's, the composition of stable nitrogen (^{15}N) and carbon (^{13}C) isotopes were used to estimate the trophic position of an organism as well as the source of its diet (Fry and Sherr, 1984). Minagawa and Wada (1984) and Hobson and Welch (1992) found a stepwise enrichment of ^{15}N with increasing trophic position of 3-5 ‰ $\delta^{15}N$ per trophic level, whereas the stable carbon isotope ^{13}C only increased by 1-2 ‰ $\delta^{13}C$ per trophic level.

In this chapter, we will describe the distribution, composition, and trophic position of gelatinous zooplankton in the northern BUS to test the following hypothesis:

Distinct differences exist between inshore and offshore communities.

(i) Inshore, in the centre of the upwelling region, more and larger organisms with less taxonomical diversity than in the oceanic offshore region are expected.

(ii) Inshore, a more classical short food-chain exists, whereas a more complex food web exists offshore. These differences are also reflected by the trophic level of the gelatinous organisms, with higher trophic levels offshore.

SAMPLING AND ANALYSIS

Sampling was conducted on an inshore/offshore transect off Walvis Bay (Namibia) in the northern BUS (23°S; 14° -11° 5'E) on cruise MSM07/2 of *RV Maria S. Merian* in March 2008 (five stations: offshore, slope, outer and inner shelf, coastal; Figure 1, Table 1) and on cruise 258 of *FRS Africana* in December 2009 (four stations: offshore, shelf break, outer and inner shelf; Figure 1, Table 1). Fine-stratified samples were taken down to 1000 m depth by oblique hauls (towing speed: 2 knots) with a $1m^2$-Double-MOCNESS in 2008 and a 1 m^2-Single-MOCNESS in 2009 (Multiple Opening and Closing Net and Environmental Sensing System; Wiebe et al., 1985) equipped with 20 or 9 nets of 333 µm mesh aperture, respectively. The single nets can be sequentially opened and closed at defined depths (Table 1). The Double-MOCNESS is constructed of two single systems side by side. Water depths increased from 60 m to 3060 m on the inshore/offshore transect. Veering and heaving speed of the winch was ca. 0.5 $m\ s^{-1}$. The speed was reduced to 0.2-0.3 $m\ s^{-1}$ in the upper 200 m. The mean filtered volumes per net were 638 m^3 for the samples below 200 m and 143 m^3 for the samples above 200 m. The surface net failed in haul MOC-1-8 during the Africana cruise in December 2009; sampling was only obtained between 22 and 25 m depth with this net. Upon recovery of the MOCNESS, the nets were rinsed with seawater and plankton was preserved in a 4% formaldehyde-seawater solution buffered with sodium-tetraborate (Steedman, 1976) for biomass and taxonomic analyses.

Table 1. Station data and sampled depth intervals of the MOCNESS hauls. WB= Walvis Bay. Local time = UTC +2h.

Cruise	Haul	Station	Date	Sampling time (UTC)	Lat.	Long.	Water depth (m)	Sampled depth range and intervals (# of samples)
Maria S. Merian 07/2 March 2008	MOC-D-1	WB-M1 offshore	10.03.2008	07:20 - 09:45	22°59’S	11°52’E	2933	0-25-50-100-150-200-400-600-800-1000 m (9)
	MOC-D-2	WB-M2 slope	11.03.2008	00:28 - 02:40	22°59’S	12°48’E	920	0-25-50-100-150-200-400-600-800 m (8)
	MOC-D-3	WB-M3 outer shelf	11.03.2008	10:55 - 11:40	22°59’S	13°33’E	216	0-25-50-100-150m (4)
	MOC-D-4	WB-M4 inner shelf	11.03.2008	18:03 - 18:20	23°01’S	14°00’E	137	0-25-50-75-100 m (4)
	MOC-D-5	WB-M5 coastal	11.03.2008	23:22 - 23:43	23°01’S	14°14’E	105	0-25-50-75 m (3)
Africana 258 December 2009	MOC-1-8	WB-A1 offshore	12.12.2009	19:35 - 21:00	22°58’S	11°40’E	3142	22-25-50-100-200-300-400-500-650 m (8)
	MOC-1-9	WB-A2 shelf break	13.12.2009	12:40 - 13:35	23°00’S	13°16’E	361	0-25-50-100-200-300 m (5)
	MOC-1-10	WB-A3 outer shelf	13.12.2009	17:35 - 18:00	23°00’S	13°41’E	145	0-25-50-100 m (3)
	MOC-1-11	WB-A4 inner shelf	13.12.2009	23:10 - 23:30	23°00’S	14°05’E	122	0-25-50-100 m (3)

Table 2. The results of the stable isotope analyses for each of specific taxa. F = Freeze-dryer, D = Drying oven. Local time = UTC +2h. WB = Walvis Bay, RP = Rocky Point, K = Kunene, T = Lüderitz. MOC = MOCNESS, PT = Pelagic Trawl, MCN = Multiple Closing Net, TT = Tucker Trawl, DN = Driftnet, WP-2 = WP-2 Net.

Species/ Group	Station	Date	UTC Start	Gear	Depth	drying method	$\delta^{15}N$	$\delta^{13}C$
Pelagia noctiluca	RP-3	08.12.2009	18:17	MOC	0-90	F	8.67	-14.54
Pelagia noctiluca	RP-3	08.12.2009	18:17	MOC	0-90	D	9.58	-14.86
Aequorea spp.	RP-3	08.12.2009	18:17	MOC	90-50	D	14.57	-14.50
Aequorea spp.	RP-3	08.12.2009	18:17	MOC	90-50	F	11.43	-14.16
Aequorea spp.	T6	06.12.2009	03:24	PT		F	9.49	-13.78
Aequorea spp.	T6	06.12.2009	03:24	PT		D	10.36	-16.65
Boroe spp.	K-3	10.12.2009	01:30	MCN	300-100	F	8.19	-16.68
Chrysaora hysoscella	Test	08.12.2009	08:16	MOC	50	F	10.68	-15.60
Chrysaora spp.	WB-A4	13.12.2009	23:10	MOC	0-100	F	12.21	-14.25
Chrysaora spp.	WB-A4	13.12.2009	23:10	MOC	0-100	D	12.94	-14.93
Pelagia noctiluca	Test	08.12.2009	08:16	MOC	50	F	9.66	-17.10
Leptomedusae	RP-2	09.12.2009	21:55	MOC	0-330	F	9.03	-15.00
Atolla spp.	K-1	10.12.2009	19:30	MOC	650-500	F	8.06	-16.27
Abylopsis tetragonata	RP-2	09.12.2009	21:55	MOC	0-330	F	8.00	-17.23
Narcomedusae	RP-1	11.12.2009	12:30	TT	100-250	F	9.95	-15.31
Haliceras spp.	RP-2	09.12.2009	21:55	MOC	0-330	F	10.17	-14.07
Physophora hydrostatica	K-3	10.12.2009	02:30	TT	100-200	F	8.35	-17.31
Pelagia noctiluca	WB-A3	13.12.2009	16:55	WP-2	0-100	F	10.55	-18.43

Species/ Group	Station	Date	UTC Start	Gear	Depth	drying method	δ^{15}N	δ^{13}C
Pelagia noctiluca	WB-A5	14.12.2009	01:50	MCN	0-50	F	11.08	-18.33
Discomedusa lobata	RP-3	08.12.2009	17:45	TT	60-20	F	10.92	-15.57
Chrysaora hysoscella	Test	08.12.2009	08:16	MOC	50	D	11.76	-15.70
Chrysaora hysoscella	K-1	10.12.2009	19:30	MOC	100-50	F	8.52	-14.91
Siphonophora	WB-A1	12.12.2009	22:50	DN	0-2	D	9.50	-16.06
Hydrozoa indef.	WB-A5	14.12.2009	01:50	MCN	0-50	D	11.45	-18.80
Trachymedusae	RP-1	11.12.2009	13:00	MOC	0-700	D	11.28	-16.43
Hydrozoa indef.	K-3	10.12.2009	02:30	TT	100-200	D	8.51	-16.03
Hydrozoa mixsample	WB-A1	12.12.2009	23:55	WP-2	0-600	D	10.15	-18.77
Siphonophora mixsample	WB-A1	12.12.2009	23:55	WP-2	0-600	D	10.28	-17.94
Siphonophora mixsample	WB-A2	13.12.2009	11:48	WP-2	0-300	D	8.79	-16.89
Hydrozoa mixsample	WB-A2	13.12.2009	11:48	WP-2	0-300	D	8.17	-19.66
Hydrozoa mixsample	WB-A3	13.12.2009	16:55	WP-2	0-100	D	12.64	-17.91
Hydrozoa mixsample	WB-A4	13.12.2009	21:41	WP-2	0-100	D	12.81	-16.29
Ctenophora	WB-A4	13.12.2009	21:41	WP-2	0-100	D	10.71	-17.75
Hydrozoa mixsample	WB-A5	14.12.2009	02:28	WP-2	0-50	D	10.50	-19.12

Table 3. δ^{15}N values (‰) and TN= Total N (μgL^{-1}) of suspended particles from 8 sites in the Namibian upwelling region in December 2009. WB = Walvis Bay, RP = Rocky Point, K = Kunene.

Station	K-2		K-4		K-5		RP-1		RP-2		RP-3		WB-A1		WB-A2		WB-A3		WB-A4		WB-A5	
Lat.	17°15’S		17°15’S		17°14’S		18°59’S		19°00’S		19°00’S		22°58’S		22°59’S		23°00’S		23°00’S		23°00’S	
Lon.	10°46’E		11°30’E		11°47’E		10°30’E		11°25’E		12°15’E		11°43’E		13°14’E		13°40’E		14°04°E		14°19’E	
Depth (m)	δ^{15}N	TN	δ^{15}N	TN	δ^{15}N	TN	δ^{15}N	TN	δ^{15}N	TN	δ^{15}N	TN	δ^{15}N	TN	δ^{15}N	TN	δ^{15}N	TN	δ^{15}N	TN	δ^{15}N	TN
0	3.23	54.02					7.41	37.06			7.17	65.67	6.13	26.36	4.91	41.64	7.30	83.50	6.02	79.46	8.84	118.23
10	3.03	27.43							7.16	41.92	6.54	56.84			5.79	45.87			5.79	40.01		
15			2.89	13.15													6.48	58.25				
20			2.48	15.27					6.06	33.44	7.76	18.09			5.60	39.66			6.51	22.32	11.97	82.66
25	3.23	45.22											6.19	20.24								
30											7.68	14.83							7.13	16.36		
35					3.77	29.87																
40																			8.22	7.55	5.12	21.01
50	4.15	17.77											6.89	19.02	7.07	12.83						
weighted mean	3.31		2.67		3.77		7.41		6.67		7.06		6.37		5.59		6.96		6.24		9.65	

Table 4. List of Medusae and Ctenophora species recorded in the Walvis Bay transect listed in taxonomical order according to Bouillon (1999) for Hydromedusae and to Mianzan and Cornelius (1999) for Scyphozoa. The abundance is integrated over the whole water column sampled with the MOCNESS. - = absent; + = 0-10 ind. 1000 m^{-3}; ++ = 10-100 ind. 1000 m^{-3}; +++ = 100-1000 ind. 1000 m^{-3}; ++++ = >1000 ind. 1000 m^{-3}.

	March 2008					December 2009			
Taxon	offshore	slope	outer shelf	inner shelf	costal zone	offshore	shelf-break	outer shelf	inner shelf
indef. Hydrozoa	+	-	-	-	-	++	+++	+++	++
indef. Anthomedusae	++	-	-	++	-	+	+	++	++
Bythotiara murrayi Günther (1903)	-	-	-	-	-	-	+	-	-
Leukartiara spp. Hartlaub (1913)	-	-	-	+	-	-	+	-	+
indef. Leptomedusae	+	-	-	+	-	++	++	+	-
Aequorea spp. Péron and Lesueur (1810)	-	-	++	+	++	+	-	+	+
Obelia spp. Péron and Lesueur (1810)	-	-	++	+	++++	-	-	-	+++
Clytia spp. Lamouroux (1812)	-	-	-	+	+++	-	-	+	-
Proboscidactyla menoni Pagès et al. (1991)	-	-	-	-	-	-	-	-	++
Proboscidactyla spp. Schuchert (1996)	-	-	-	+	+++	-	-	-	-
indef. Narcomedusae	-	-	-	-	-	+	+	-	-
Solmundella bitentaculata Quoy and Gaimard (1833)	++	+	-	++	-	+	+	++	-
indef. Trachymedusae	+	+	-	-	-	++	+	-	-
Liriope tetraphylla Chamisso and Eysenhardt (1821)	++	+	-	-	-	++	+++	+++	-
Haliceras minima Fewkes (1882)	+	+	-	-	-	+	-	-	-
Aglaura hemistoma Péron and Lesueur (1810)	+++	++	+	-	-	++	-	+	-
Arctapodema spp. Dall (1907)	-	-	-	-	-	-	+	-	-
Rhopalonema velatum Gegenbaur (1857)	-	+	-	-	-	-	-	-	-
Pelagia noctiluca Foskål (1775)	-	-	-	-	+	-	-	-	-
Chrysaora hysoscella Linné (1766)	-	-	-	++	++	-	-	+	-
Atolla spp. Haeckel (1880)	+	+	-	-	-	+	-	-	-
inc. sed. *Tetraplatia volitans* Busch (1851)	+	+	-	-	-	++	+	-	-
Beroe sp. Browne (1756)	+	-	-	-	-	+	+	-	-
Total no. of Medusae and Ctenophora groups	11	9	3	9	6	13	12	9	6

Table 5. List of Siphonophora species recorded in the Walvis Bay transect listed in taxonomical order according to Pugh (1999). The abundance is integrated over the whole water column sampled with the MOCNESS. - = absent; + = 0-10 parts 1000 m^{-3}; ++ = 10-100 parts 1000 m^{-3}; +++ = 100-1000 parts 1000 m^{-3}; ++++ = >1000 parts 1000 m^{-3}.

	March 2008					December 2009			
Taxon	offshore	slope	outer shelf	inner shelf	costal zone	offshore	shelf-break	outer shelf	inner shelf
indef Siphonophorae	-	++	-	-	-	+	+++	++	+
indef. Agalmatidae	+++	+++	++++	++++	++++	+++	++++	++++	+++
Aglama spp. Eschscholtz (1825)	-	-	-	-	-	+	-	-	-
Nanomia bijuga Chiaje (1841)	+	-	-	-	-	-	-	-	-
Physophora hydrostatica Forskål (1775)	-	+	-	-	-	++	++	++	-
Forskalia leuckarti Bedot (1893)	-	++	+	+	-	++	+++	++++	++
indef. Prayidae	++	++	++	-	-	++	++	-	-
indef Hyppopodiidae	+	-	-	-	-	-	-	-	-
Vogita spp. Kölliker (1853)	+	+	-	-	-	+	-	-	-
indef Abylidae Agassiz (1862)	+	+	-	-	-	++	+	-	-
indef Diphyidae	+++	+++	+++	++++	++++	++++	+++	++	++
Sulculeolaria biloba Sars (1846)	+	-	-	-	-	-	-	-	-
Chelophyes appendiculata Eschscholtz (1829)	+	+	-	-	-	-	-	-	-
Eudoxoides spiralis Bigelow (1911)	+	+	-	-	-	-	-	-	-
Eudoxoides mitra Huxley (1859)	++	-	-	-	-	+	-	-	-
Lensia spp. Totton (1932)	++	+	-	-	-	+	-	-	-
Dimophyes arctica Chun (1897)	+	-	-	-	-	-	-	-	-
Muggiaea spp. Busch (1851)	+	-	-	-	-	+	-	-	-
Total no. of Siphonophora groups	14	11	4	3	2	12	7	5	4

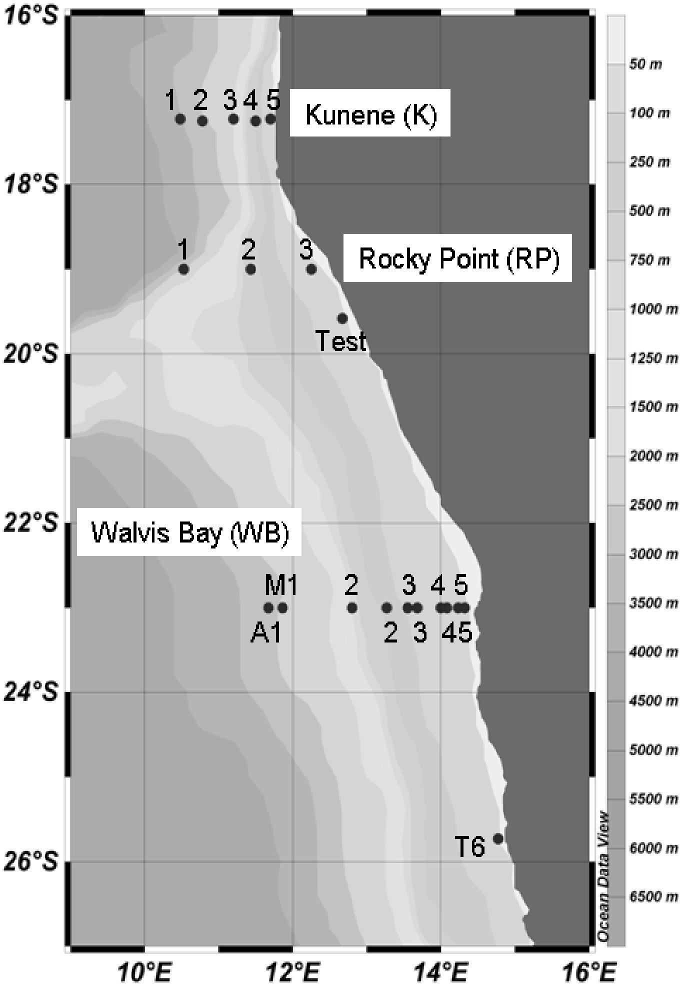

Figure 1. The study area off northern Namibia. The station numbers correspond to the station names in Tables 1 and 2.

In the laboratory, the preserved zooplankton samples for biomass determination and taxonomic analyses were sieved into fractions of <0.5, 0.5-1, 1–2, 2–5 and >5 mm. After placing the fractions in 70% ethanol for 30 s and drying them on tissue paper, the material was wet weighed on an analytical balance. Instead of a more precise dry weight determination, this method allowed a subsequent taxonomical analysis. After weighing, the samples were transferred into a sorting fluid composed of 0.5% propylenephenoxetol, 5.0% propylene-glycol and 94.5% fresh water (Steedman, 1976). Rich zooplankton samples were split according to Kott (1953). The gelatinous zooplankton was removed from the fractionated samples for further analyses. Gelatinous zooplankton was sorted into taxonomic groups and cnidarians and ctenophores were identified at species level, if possible. Due to their behaviour to live in colonies, which break into pieces when caught with plankton nets, Siphonophora were not included in the total counts of Cnidaria. The abundance of Siphonophora and other Coelenterata is expressed as parts 1000 m^{-3} or ind. 1000 m^{-3}, respectively.

Samples for stable isotope analyses were taken with different plankton nets (MOCNESS, WP-2 with a modified bucket to minimize the damage of the animals, Multinet, Driftnet, Tucker Trawl and Pelagic Trawl) at 12 stations in the Benguela Current Region during the cruise in 2009 (Figure 1 and Table 2).

The samples were frozen at -20° C directly after sampling. All samples were defrosted in the laboratory, weighted with an accuracy of 1 mg with an analytical balance, washed with fresh water and dried, either in a freeze-dryer at -40 °C for at least 24 h or in a drying oven at 60° C for at least 48h (see Table 2). Afterwards, the dried samples were pulverized using pestle and mortar. No further treatment was applied to the samples.

Stable isotope analyses and concentration measurements of nitrogen and carbon were performed simultaneously with a THERMO/Finnigan MAT V isotope ratio mass spectrometer, coupled to a THERMO Flash EA 1112 elemental analyzer via a THERMO/Finnigan Conflo III-interface at the stable isotope laboratory of the Museum für Naturkunde, Berlin. Stable isotope ratios were expressed in the conventional delta notation ($\delta^{13}C$ and $\delta^{15}N$) relative to VPDB (Vienna PeeDee Belemnite standard) and atmospheric nitrogen (Mariotti, 1983).

$$\delta^{13}C \text{ or } \delta^{15}N \text{ (‰)} = ((R_{sample} / R_{standard}) - 1) * 1000$$

where R is the ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$ of the sample or the standard. Standard deviations for repeated measurements of lab standard material (peptone) were generally better than 0.15 ‰ for nitrogen and carbon, respectively. Standard deviations of concentration measurements of replicates of lab standards were <3% of the concentration analysed.

The $\delta^{15}N$ values of suspended particulate organic matter (POM) were measured in water samples from different depths at 11 stations (Figure 1,

Table 3) in the northern BUS. The material was taken with a rosette sampler in December 2009 during Africana cruise 258.

Water amounts of 2 to 21 litres (depending on total suspended matter concentrations) were immediately filtered on pre-combusted (450°C overnight) and pre-weighed GF filters (diameter: 47 mm; pore size ~0.7 µm). Filters were subsequently dried at 40°C overnight and stored dry and cool until further analyses for stable nitrogen isotopes ($\delta^{15}N$) with an isotope ratio mass spectrometer (THERMO/Finnigan MAT 252), coupled to a Carlo Erba EA 2500 elemental analyser via a THERMO/Finnigan Conflo III-interface. The weighted mean (WM) was calculated for all sampled depths (*i*) in the upper 50 m at each station with total nitrogen (TN) as weighting factor using the following formula:

$$WM = \frac{\sum_{i=1}^{n}(TN_i * \delta^{15}N_i)}{\sum_{i=1}^{n}(TN_i)}$$

Although the increase in $\delta^{15}N$ between trophic levels can be variable (McCutchan et al., 2003), a mean trophic fractionation of 3.4 ‰ is widely applicable (Minagawa and Wada, 1984; Hobson and Welch, 1992; Post, 2002). The trophic level (TL) of the different zooplankton groups can be calculated by the following formula:

$$TL = \frac{\delta^{15}N_{Zoo} - \delta^{15}N_{Sus}}{3.4} + 1$$

where $\delta^{15}N_{Zoo}$ and $\delta^{15}N_{Sus}$ are the stable isotope values of gelatinous zooplankton and suspended material, respectively.

Vertical Distribution

The vertical distribution of Hydrozoa, Siphonophora parts, Scyphozoa and Ctenophora revealed highest concentrations of single individuals of the state jellyfish (Siphonophora) at all stations followed by Hydrozoa, Scyphozoa and Ctenophora (Figure 2).

Generally, highest concentration was detected in the surface or subsurface layers. Below this depth, the abundance declined. Hydrozoa and Siphonophora showed more or less stable concentrations below 200-300 m at the offshore and slope stations. Distinct differences between the two investigated seasons were not visible.

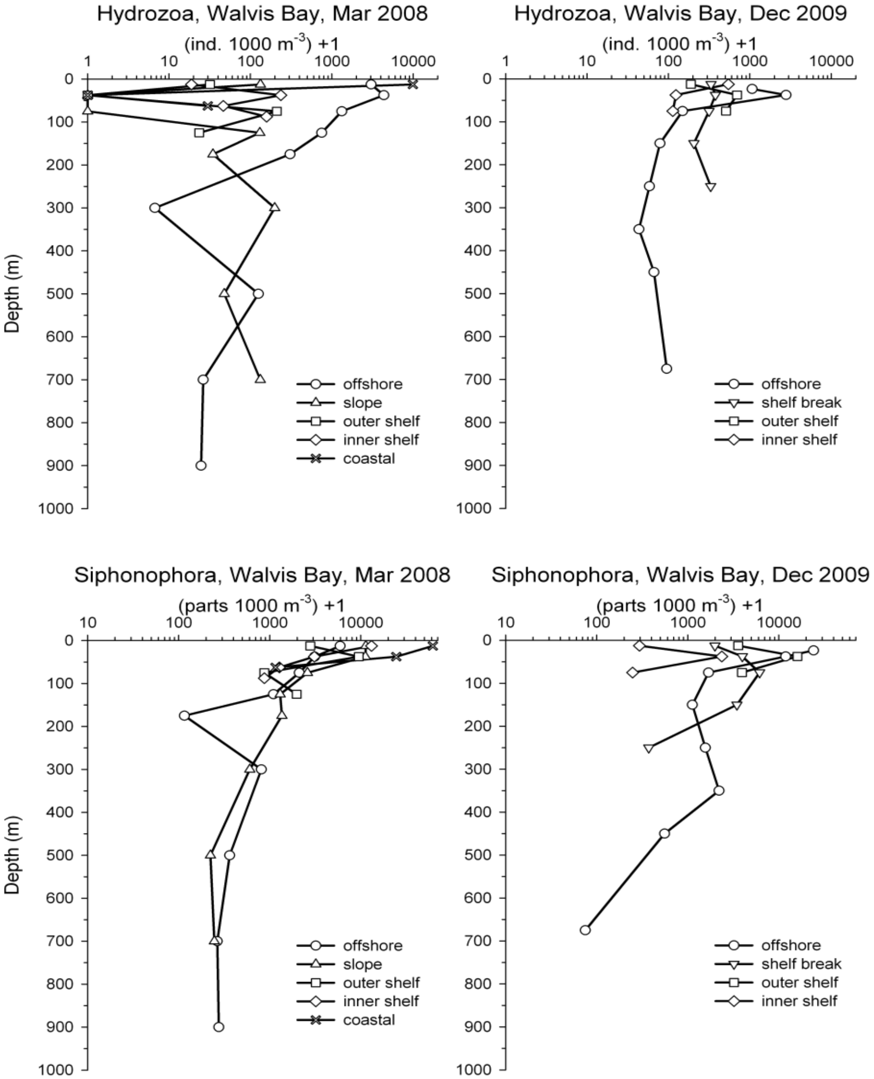

Figure 2. (Continued).

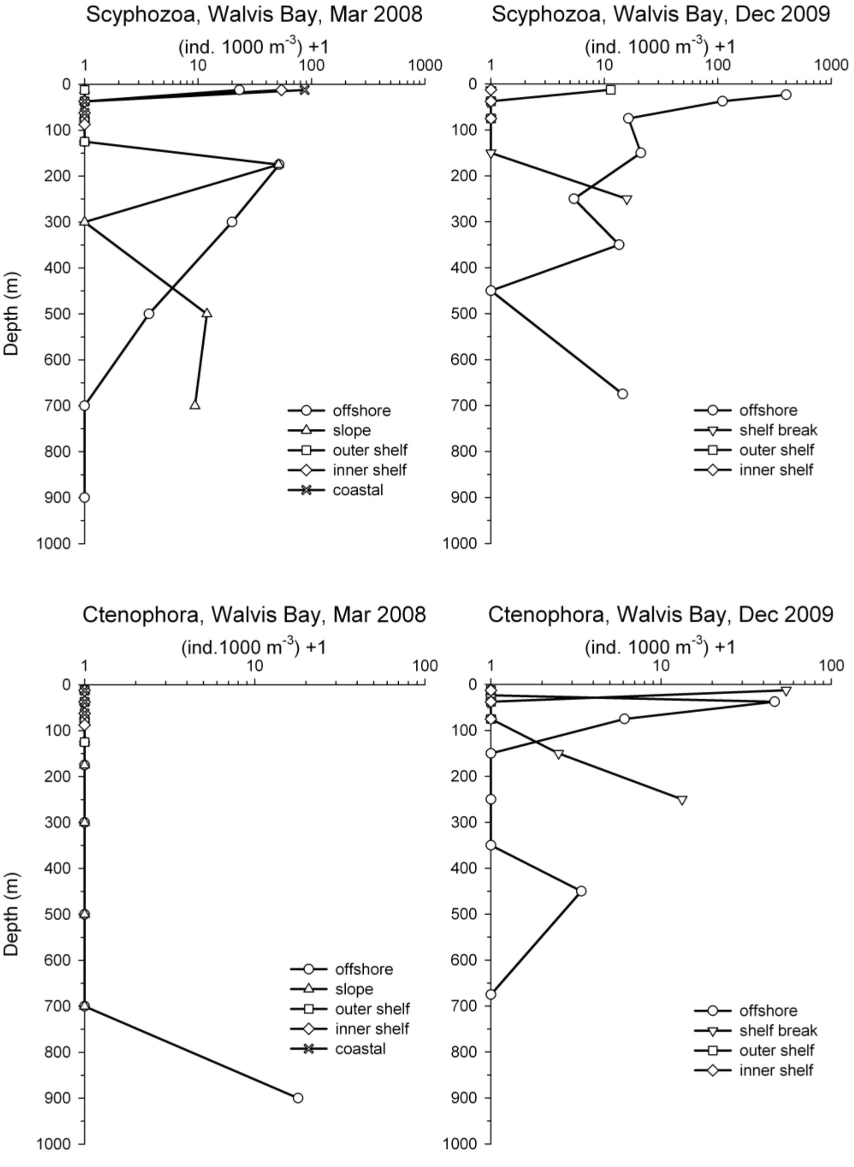

Figure 2. Vertical distribution of Hydrozoa, Siphonophora parts, Scyphozoa and Ctenophora in March 2008 and December 2009.

Taxonomic Composition and Abundance

A total of 40 Cnidaria taxa (22 Medusae, 18 Siphonophora) were detected during both cruises (Figure 3), 35 taxa were sampled along the transect in March 2008 (18 Medusae, 17 Siphonophora) and 31 taxa in December 2009 (19 Medusae, 12 Siphonophora). One species of Ctenophora (*Beroe* sp.) was found in both years at the offshore stations and also in December 2009 at the shelf-break station. The diversity increased from inshore to offshore in both years (see Tables 4 and 5).

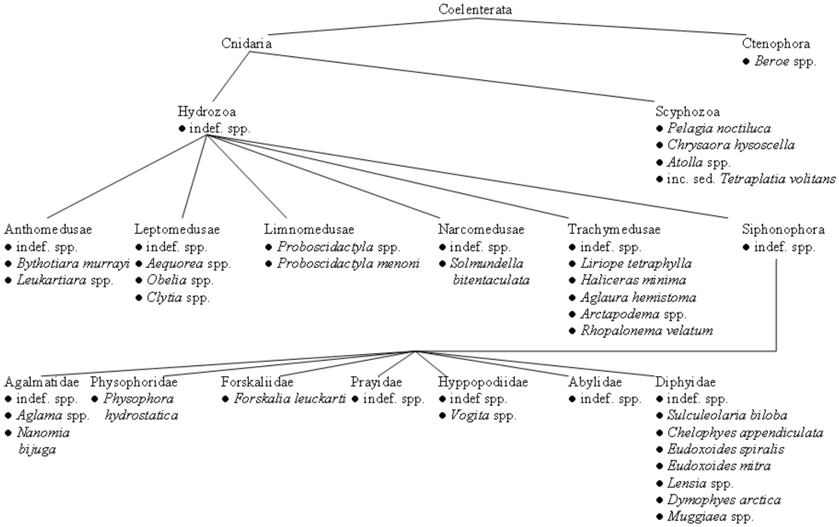

Figure 3. Taxonomic position of detected (●) Coelenterata.

Hydrozoa were sometimes in bad condition and could not be exactly specified (Hydrozoa indef.; Figure 3, Table 4). The subclass Anthomedusae showed no clear horizontal distribution pattern in both years, but this group was found at more stations (inshore and offshore) and in higher abundance in December 2009.

Aequorea aequorea, *Obelia* spp. and *Clytia* spp. occurred at the shelf stations and also at the costal station with high abundances of more than 100 ind. 1000 m^{-3} in 2008. Not further identified species of the subclass Leptomedusae were detected offshore.

Only one genus of Limnomedusae (*Proboscidactyla*) was found at the inner shelf and costal stations. Some not identified species of the subclass

Narcomedusae were found at the shelf-break station in 2009 (0-10 ind. 1000 m^{-3}), and the species *Solmundella bitentaculata* was sampled at three stations (offshore, slope and inner-shelf in 2008 and offshore, shelf-break and outer shelf in 2009) in each year.

The subclass Trachymedusae was comprised of up to five species, *Liriope tetraphylla*, *Aglaura hemistoma*, *Haliceras minima, Arctapodema* spp. and *Rhopalonema* spp., whereas the first two had the highest abundance in both years. Trachymedusae were only sampled at the offshore, slope and outer shelf stations in 2008 with highest abundance at the offshore station (*Aglaura hemistoma* with over 100 ind. 1000 m^{-3}).

In 2009, this group was detected at the same stations, also with highest abundance at the offshore station (*Liriope tetraphylla* and *Aglaura hemistoma* with over 10 ind. 1000 m^{-3}).

Scyphozoa were sampled at only a few stations, represented by three species: *Atolla* spp. at the offshore stations during both cruises, *Pelagia noctiluca* only in the samples from March 2008 at the costal station and *Chrysaora hysoscella* at the shelf and costal stations. The inc. sed. *Tetraplatia volitans* was regularly found at the offshore and the slope stations during both cruises. Except of *Tetraplatia volitans*, the maximum abundance of all species was below 100 ind. 1000 m^{-3}.

Siphonophora were present at all stations during both cruises, however, most of the individuals could only be identified on the family level (Table 5). Diphyidae and Agalmatidae were collected at all stations with abundances over 100 parts 1000 m^{-3} during both cruises. *Forskalia leukati* occurred regularly in high abundances between 10 and more than 1000 parts 1000 m^{-3}. Additionally to these families and species, *Physophora hydrostatica*, Hyppopodiidae, Prayidae and Abylidae were detected at the offshore, slope and outer shelf stations.

Relative Composition

The relative taxonomical composition of the gelatinous zooplankton changed from offshore to inshore and from year to year (see Figure 4a). In both years, the offshore, slope and shelf-break stations were dominated by Trachymedusae (82 and 87 % in 2008; 66 and 36 % in 2009) with decreasing importance from offshore to inshore.

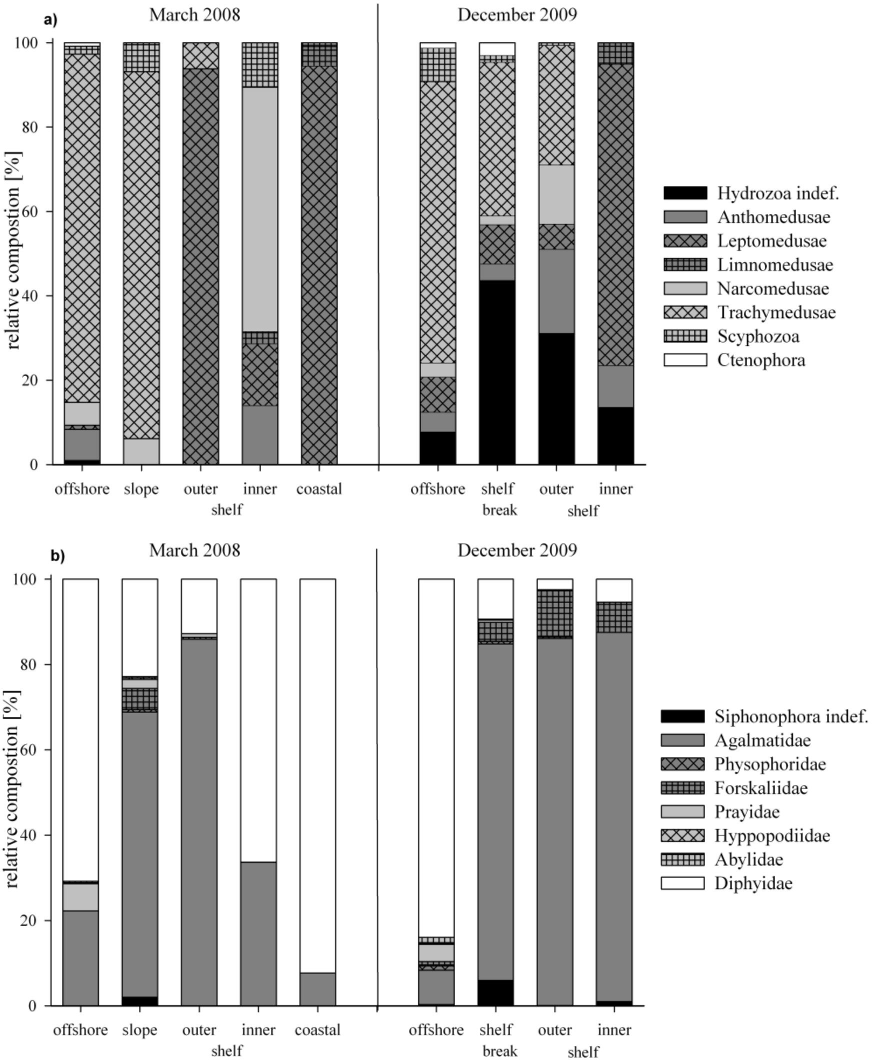

Figure 4. Relative composition of Medusae (a) and Siphonophora (b) at the different stations and sampling periods on the Walvis Bay transect.

Anthomedusae had their highest abundance at the inner shelf station in 2008 (14 %) and at the outer shelf station in 2009 (20 %).

Leptomedusae increased from offshore to inshore in both years (from 1 % to 94.5 % in 2008 and from 8 % to 71 % in 2009). Limnomedusae were only found at the inner shelf stations and at the costal station.

Narcomedusae revealed different horizontal patterns in the two years: they were found with relative abundances of 5 and 6 % at the offshore and slope stations and with 58 % at the inner shelf station in 2008. In 2009, however, they were only detected at the offshore, shelf-break and outer shelf stations with proportions of 3 % (offshore) and up to 14 % (outer shelf).

Scyphozoa showed no clear horizontal pattern in 2008; they were found at all stations except the outer shelf station. The highest proportion occurred at the inner shelf station with 10 %. In 2009, the relative contribution decreased from 8 % at the offshore station to 0.5 % at the outer shelf station. No Scyphozoa species were detected at the inner shelf stations. Ctenophora were only found at the offshore station in 2008 and at the offshore and shelf-break stations in 2009.

The relative taxonomical composition of the Siphonophora was similar during both years of investigation (Figure 4b). The relative importance of Agalmatidae increased from 22 % in 2008 and 8 % in 2009 (offshore) to 86 % in 2008 and 2009 (outer shelf).

Diphyidae were also an important family of Siphonophora. The relative abundance of this family was highest at the costal station with 92 % and lowest at the outer shelf with 13 % in 2008. All other families contributed with proportions less than 6 %, whereas Prayidae, Hyppopodiidae and Abylidae were found further offshore and Forskaliidae and Physophoridae occurred inshore.

In 2009, Diphyidae were most abundant at the offshore station (84 %), decreasing to 10% at the shelf-break, 2.5 % at the outer shelf, and 5.5 % at the inner shelf stations.

Size Class Composition

The relative composition of the size classes of the Medusae showed a shift from smaller organisms (highest shares in the 0.5-1 mm and the 1-2 mm fractions, Figure 5a) at the offshore, slope and shelf-break stations, to larger organisms at the costal and the inner and outer shelf stations (highest shares in the 1-2 mm, 2-5 mm and >5 mm fractions; Figure 5a). This trend was not detected for Siphonophora parts (Figure 5b).

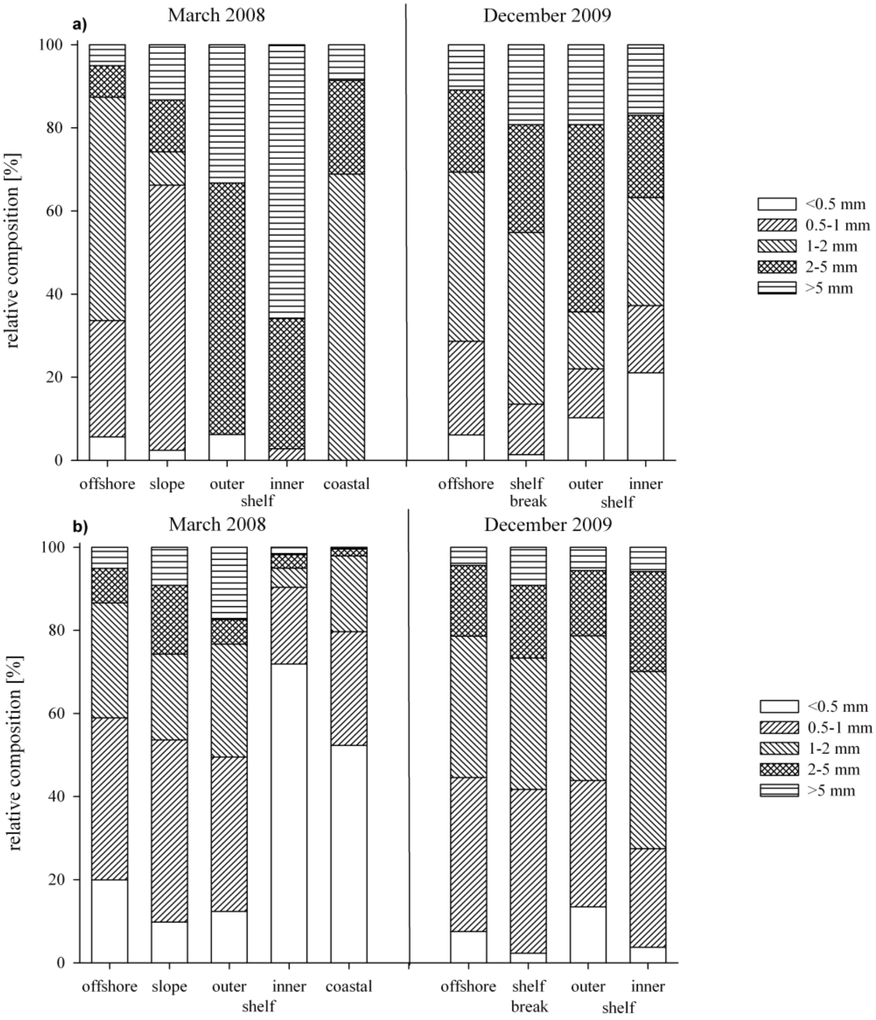

Figure 5. Relative composition of the different size classes of Medusae (a) and Siphonophora (b) at the different station and sampling periods on the Walvis Bay transect.

Stable Isotopes

The stable carbon isotope values ($\delta^{13}C$) of gelatinous zooplankton ranged from -19.6 ‰ for Hydrozoa indef. to -13.7 ‰ for Leptomedusae. Stable nitrogen isotope values ($\delta^{15}N$) of gelatinous zooplankton ranged from 8 ‰ for

Siphonophora to 14.5 ‰ for Leptomedusae. The mean δ^{15}N values decreased from 11.6 ‰ (±0.9 ‰) at the shelf stations to 8.4 ‰ (±0.4 ‰) at the shelf-break station (Figure 6a) on the Walvis Bay transect. Further north at the Rocky Point transect the mean values for δ^{15}N decreased from 11 ‰ (± 2.2 ‰) at the shelf station to 9 ‰ (±1 ‰) at the shelf-break station. At the Kunene transect, the lowest δ^{15}N mean values of 8.2 ‰ (±0.3 ‰) and 8.4 ‰ (±0.3 ‰) were measured at the offshore sand shelf-break stations, respectively.

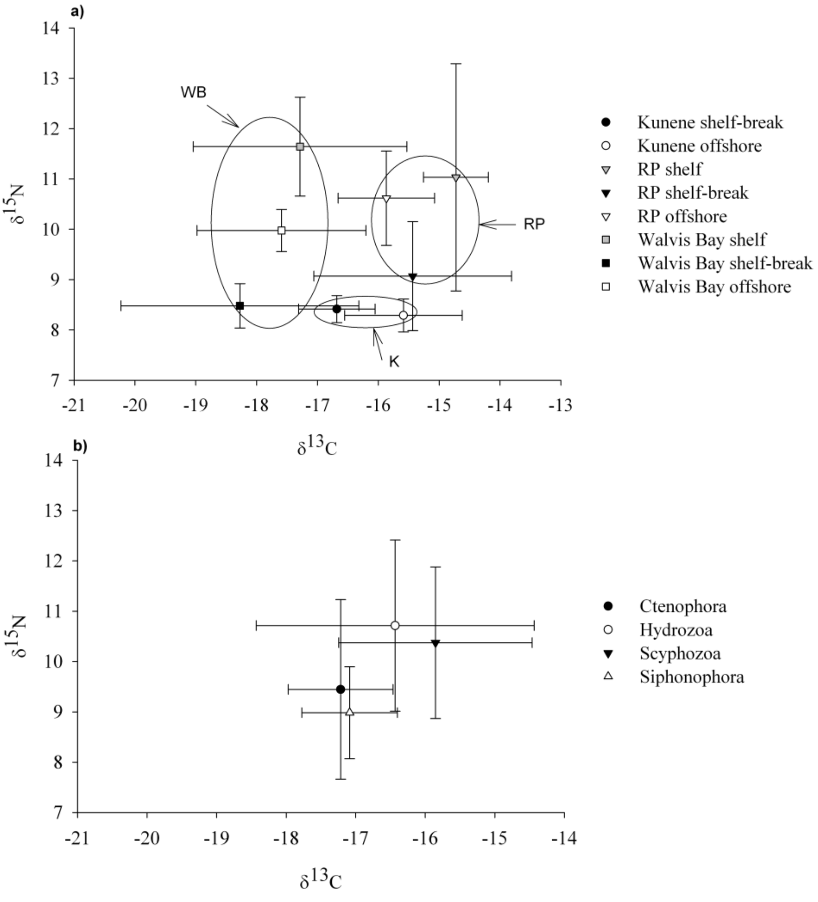

Figure 6. Relationship between stable nitrogen (δ^{15}N) and stable carbon (δ^{13}C) isotopic signatures of gelatinous zooplankton at different locations (a) and for different taxonomical groups (b). Mean values and standard deviations are shown. WB = Walvis Bay, RP = Rocky Point, K = Kunene.

Differences in $\delta^{13}C$ were detected between the three transects. On the Walvis Bay transect, the values of $\delta^{13}C$ varied between -18.3 ‰ and -17.2 ‰. Slightly higher values (-15.8 ‰ to -14.7 ‰) were detected on the Rocky Point transect, whereas slightly lower values (-16.6 ‰ and -15.5 ‰) were again detected on the Kunene transect (Figure 6a).

The different taxonomical groups also showed high deviations in their stable isotope signature. The highest $\delta^{15}N$ value was measured for the Hydrozoa with 10.7 ‰ (±1.7) and the lowest $\delta^{15}N$ value was measured for Siphonophora with 8.9 ‰ (±0.9) (Figure 6b). However, no significant differences (Kruskal-Wallis test) were detected between these taxonomical groups. Additionally, the C:N ratio was calculated from the carbon and nitrogen molar concentration. The lowest C:N ratio of 4.7 (±0.3) was found for Scyphozoa, a C:N ratio of 5.0 (±0.3) for Siphonophora and a ratio of 5.7 (±2) for Hydrozoa was measured, Ctenophora showed the highest C:N ratio of 6.5 (±1) and were close to the Redfield ratio of 6.6 (Redfield et al., 1963).

The stable nitrogen isotopes ($\delta^{15}N$) data for suspended material also showed a north-to-south variability (Tab. 3). The lowest values of $\delta^{15}N$ (3.3 ‰) were measured offshore on the Kunene transect (K-2) and at the shelf-break station (2.7 ‰). On the Rocky Point transect, the values were between 7.4 ‰ at the offshore station and 6.7 ‰ at the shelf-break station. Similar values between 5.6 ‰ at the shelf-break station and 7.0 ‰ at the outer shelf station were measured on the Walvis Bay transect. The single high value of 9.7 ‰ at the costal station was considered as an outlier.

CONCLUSION

There is some evidence that the abundance of gelatinous organisms increased during the last decades in the northern Benguela Current System (Brotz et al., 2012; Flynn et al., 2012). However, concentrations may vary seasonally and spatially (Flynn et al., 2012), which can be related to the different productivity regimes and seasonal changes in upwelling intensity. Upwelling intensity was weak during the sampling periods in 2008 and 2009 (Martin et al. in revision), which may explain the lack of seasonal differences in our study. The main aim of our study was to investigate the distribution and trophic position of small gelatinous organisms. However, analysing gelatinous zooplankton with net samples is difficult due to the loss of material through meshes, while large gelatinous organisms, mainly Cnidarians, may clog the nets during sampling. But the biggest problem is that most of the taxonomical characteristics are destroyed. By rinsing and sieving the samples many taxonomical characteristics are damaged which hampers the identification at species level. Whole Siphonophora colonies can be destroyed during sampling and only parts can be collected in the nets. Nevertheless, such analyses were also successfully done by other authors (e.g. Pagès and Gili, 1991; Pagès, 1992; Gibbons and Buecher, 2001; Buecher and Gibbons, 2003) and the analyses of gelatinous organisms with net samples are considered to provide very interesting results.

Pagès (1992) found a distribution similar to our study for Medusae in the Benguela Current System during cruises in December 1981 and March 1982 using a Bongo net with 57 cm mouth diameter and 500 and 300 µm mesh size (Table 6 and 7). In our study, Trachymedusae were also mainly found offshore. *Liriope tetraphylla* and *Aglaura hemistoma* were most abundant in both studies. Pagès (1992) defined the Limnomedusae *Proboscidactyla menoni* as shelf species and the representatives of Leptomedusae and Anthomedusae as shelf-break and shelf species. Within these groups *Clytia* spp. was the most abundant Leptomedusae on the shelf in December 1981. *Obelia* spp. was the most abundant Leptomedusae on the shelf in March and *Mitrocomella grandis* was the most abundant shelf-break species. In our study, the most abundant Leptomedusae species in March 2008 and December 2009 was *Obelia* spp. Hydroidpolyps of *Obelia* spp. were also very abundant on a mooring recovered at the shelf-break in October 2010 (pers. obs.). The Scyphozoa *Chrysaora hysoscella* was of minor importance (Table 6). Pagès (1992) found a very high abundance of the latter species but included data of the Sea Fisheries Research Institute in Cape Town to the abundance data of this species as well as for the Leptomedusae *Aequorea aequorea*. These Medusae were collected using large trawl nets, which probably sampled higher amounts of this large jellyfish.

The distribution of Siphonophora presented by Pagès (1992) was different to the distribution found in our study (Table 7). The author stated that the Diphyidae *Muggiaea atlantica* was the most abundant species with 877 parts 1000 m^{-3} in the upper 100 m in December 1981 and 1267 parts 1000 m^{-3} in the upper 100 m in March 1982. All other species presented by Pagès (1992) were at lower values between 11.58 to 0.02 parts 1000 m^{-3}. In our study, three of four stations were dominated by Agalmatidae and only the offshore station was dominated by Diphyidae in December 2009, whereas Diphyidae were the dominant Siphonophora at the inner shelf and costal stations in 2008. Pagès (1992) also found a higher abundance of *Muggiaea atlantica* in March than in December.

Table 6. List of Medusae species found by Pagès (1992) in the upper 100 m. - = absent; + = 0-10 parts 1000 m^{-3}; ++ = 10-100 parts 1000 m^{-3}; +++ = 100-1000 parts 1000 m^{-3}; ++++ = >1000 parts 1000 m^{-3}; n.d. = no data available

	March 1982			December 1981		
Taxon	offshore	shelf	costal zone	offshore	shelf	costal zone
indef. Hydrozoa						
indef. Anthomedusae	n.d.	n.d.	+	n.d.	n.d.	+
Bythotiara murrayi Günther (1903)	-	-	-	-	-	-
Leukartiara spp. Hartlaub (1913)	n.d.	+	n.d.	n.d.	+	n.d.
indef. Leptomedusae	n.d.	+	n.d.	n.d.	++	n.d.
Aequorea spp. Péron and Lesueur (1810)	n.d.	+	n.d.	n.d.	+	n.d.
Obelia spp. Péron and Lesueur (1810)	n.d.	n.d.	+	-	-	-
Clytia spp. Lamouroux (1812)	-	-	-	n.d.	n.d.	++
Proboscidactyla menoni Pagès et al. (1991)	n.d.	n.d.	+	n.d.	n.d.	++
Proboscidactyla spp. Schuchert (1996)	-	-	-	-	-	-
indef. Narcomedusae	+	n.d.	n.d.	+	n.d.	n.d.
Solmundella bitentaculata Quoy and Gaimard (1833)	+	n.d.	n.d.	-	-	-
indef. Trachymedusae						
Liriope tetraphylla Chamisso and Eysenhardt (1821)	++	n.d.	n.d.	+	n.d.	n.d.
Haliceras minima Fewkes (1882)	-	-	-	-	-	-
Aglaura hemistoma Péron and Lesueur (1810)	++	n.d.	n.d.	+	n.d.	n.d.
Arctapodema spp. Dall (1907)	-	-	-	-	-	-
Rhopalonema velatum Gegenbaur (1857)	-	-	-	+	n.d.	n.d.
Pelagia noctiluca Foskål (1775)	-	-	-	-	-	-
Chrysaora hysoscella Linné (1766)	n.d.	++		n.d.	+	
Atolla spp. Haeckel (1880)	-	-	-	-	-	-
inc. sed. *Tetraplatia volitans* Busch (1851)	-	-	-	-	-	-

Table 7. List of Siphonophora species found by Pagès (1992) in the upper 100 m. - = absent; + = 0-10 parts 1000 m^{-3}; ++ = 10-100 parts 1000 m^{-3}; +++ = 100-1000 parts 1000 m^{-3}; ++++ = >1000 parts 1000 m^{-3}; n.d. = no data available

	March 1982			December 1981		
Taxon	offshore	shelf	costal zone	offshore	shelf	costal zone
indef Siphonophorae						
indef. Agalmatidae						
Aglama spp. Eschscholtz (1825)	+	n.d.	n.d.	+	n.d.	n.d.
Nanomia bijuga Chiaje (1841)	-	-	-	-	-	-
Physophora hydrostatica Forskål (1775)	+	n.d.	n.d.	+	n.d.	n.d.
Forskalia leuckarti Bedot (1893)	+	n.d.	n.d.	+	n.d.	n.d.
indef. Prayidae	-	n.d.	n.d.	+	n.d.	n.d.
indef Hyppopodiidae	-	-	-	n.d.	+	n.d.
Vogita spp. Kölliker (1853)	-	-	-	-	-	-
indef Abylidae Agassiz (1862)	+	n.d.	n.d.	++	n.d.	n.d.
indef Diphyidae	-	-	-	-	-	-
Sulculeolaria biloba Sars (1846)	-	-	-	+	n.d.	n.d.
Chelophyes appendiculata Eschscholtz (1829)	+	n.d.	n.d.	+	n.d.	n.d.
Eudoxoides spiralis Bigelow (1911)	+	n.d.	n.d.	+	n.d.	n.d.
Eudoxoides mitra Huxley (1859)	-	-	-	-	-	-
Lensia spp. Totton (1932)	+	n.d.	n.d.	+	n.d.	n.d.
Dimophyes arctica Chun (1897)	-	-	-	-	-	-
Muggiaea spp. Busch (1851)	n.d.	n.d.	+++	n.d.	n.d.	++++

As stated in the hypothesis, we expected to find more and larger Cnidaria with less taxonomical diversity inshore, in the centre of the upwelling region, than in the oceanic offshore region. The taxonomical diversity was increasing from inshore to offshore but the abundance of species was not constantly decreasing from inshore to offshore in 2009.

In 2008, the concentration of Siphonophora was constantly decreasing from inshore to offshore, but the concentration of Medusae showed no clear trend. The highest concentration of Siphonophora and Medusae was detected at the outer shelf station in 2009, the abundance decreased from this station to the offshore station. In 2008, the highest abundance was found at the costal station. These differences may result from patterns related to upwelling filaments.

However, more data on the structure of such filaments as well as the taxonomical composition of zooplankton within the filament are necessary. The size of Siphonophora revealed no difference between the offshore and inshore stations. Within the Medusae, we found a tendency that larger organisms occurred inshore. Visual observations of many large *Chrysaora* spp., which could not have sampled quantitatively with the MOCNESS, in inshore waters support this hypothesis. In conclusion, the hypothesis of lager organisms inshore than offshore has to be rejected for the single individuals of Siphonophora but not for Medusae.

Although the taxonomy was more diverse at the offshore station, the hypothesis that a more complex food web exists offshore than inshore could not be verified based on the analysis of stable nitrogen isotopes. The $\delta^{15}N$ values showed no difference between inshore and offshore samples, but a shift in the south-north direction with higher $\delta^{15}N$ on the Walvis Bay and Rocky Point transects than at the Kunene transect. This shift was found in suspended material as well as in gelatinous zooplankton. We assume that the southern part is potentially more affected by denitrification processes which could lead to higher ^{15}N values (Nagel et al., 2013).

Moreover, under certain oceanographic conditions nitrogen fixation might be more relevant in the northern part and thus alters (decreases) ^{15}N values (Nagel et al., 2013). The Kunene River as a potential nitrogen source, however, is only of local relevance (Lahajnar in preparation). The differences in $\delta^{13}C$ indicate different sources of diet of gelatinous zooplankton for the transects. The estimated trophic position of gelatinous zooplankton (Table 8) was on the second trophic level with a slightly higher position (2.5) for the Kunene transect than for the other two transects (~2.0). These findings were supported by gut content analyses of gelatinous zooplankton (Purcell, 2003; Sabatès et al., 2010).

The authors stated that primary consumers like Copepoda were the main diet of Medusae. Differences in the trophic level between inshore and offshore gelatinous organisms were not detected.

Table 8. Mean $\delta^{15}N$ of gelatinous zooplankton and suspended material and calculated trophic level of gelatinous zooplankton. K= Kunene, RP= Rocky Point, WB= Walvis Bay.

Station (location)	Mean $\delta^{15}N$ gel. zooplankton	Mean $\delta^{15}N$ susp. material	Trophic level
K3/K4 (shelf-break)	8.41	2.67	2.7
K1/K2 (offshore)	8.29	3.31	2.5
RP-3 (shelf)	11.03	7.06	2.2
RP-2 (shelf-break)	9.07	6.67	1.7
RP-1 (offshore)	10.62	7.41	1.9
WB 3-5 (shelf)	11.64	7.62	2.2
WB-2 (shelf-break)	8.48	5.59	1.9
WB-1 (offshore)	9.98	6.37	2.1

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Chapter 8

SEASONAL DYNAMICS OF ZOOPLANKTON COMMUNITY RELATED TO THE ENVIRONMENTAL FACTORS IN A MAN-MADE SFAX SOLAR SALTERN (TUNISIA)

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ABSTRACT

The seasonal distribution of abundance of zooplankton along with the environmental factors were studied monthly, from September 2007 to August 2008, in four ponds of increasing salinity (A1: 41 psu; A5: 46 psu; A16: 67 psu; and C31: 77 psu) in the Sfax solar saltern (southeastern Tunisia). The salinity differ significantly among the four ponds (ANOVA, F = 129.62, p<0.001). A total of 21 zooplankton taxa, belonging to copepoda (17 species), rotifera (3 species), cladocera (1

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species) and others zooplankters were identified. Copepoda was the dominant group in all sampling ponds and accounted for 65% of the total zooplankton density in the Sfax solar saltern. The salinity differ significantly among the four ponds (ANOVA, F = 129.62, $p<0.001$) and the zooplankton abundance decreased with increasing salinity of the ponds. However, the highest density of total zooplankton (70.76×10^4 ind.m^{-3}) we recorded in the first pond A1 (41 psu). Differences in the density of zooplankton were found between ponds (ANOVA, F = 5.17, $p<0.01$). Total zooplankton (r = -0.355, n = 12, p = 0.05), copepods (r = -0.329, n = 12, p = 0.05) and rotifers (r = -0.592, n = 12, p = 0.05) density were negatively correlated with salinity, while positively correlated with total phosphorus (r = 0.481, n = 12, p = 0.05), (r = 0.561, n = 12, p = 0.05) and (r = 0.613, n = 12, p = 0.05), respectively.

Keywords: Sfax solar saltern, zooplankton community, environmental factors

INTRODUCTION

Zooplankton organisms play an important key role in the aquatic food webs as primary grazers of phytoplankton and as food to higher trophic organisms including the larvae of many commercial or recreational fishery species (Russell et al., 2010; Andrew et al., 2013; Johan et al., 2013). Zooplankton occupies a key position in the food web architecture (Liu and Dagg, 2003; Dagg et al., 2004). Indeed, zooplanktonic organisms constitute a major part of the diet of many fish, either throughout their life or, at least, during early ontogenic stages (Head and Pepin, 2010; Brucet et al., 2005), while also they constitute an important food source for many aquatic organisms (Beaugrand, 2008; Frank et al., 2005), such as protozoa, cladocera, copepoda, rotifera, and others which also may serve as indicators of water quality (Davies and Otene, 2009). A variety of both biotic and abiotic factors have been implicated in determining the boundaries of species distributions. Thus, the composition and abundance of zooplankton are related to many factors, such as water hydrochemistry, season, salinas morphology, presence of macrophytes, predators (Bozkurt and Guven, 2009). On the other hand, certain studies indicate that physical and chemical factors influence the distribution of zooplankton (Akin-Oriola, 2003; Ahmadi et al., 2005), copepods (Badosa et al., 2006; Hannachi et al., 2011; Abdennadher et al., 2012; Kobbi-Rebai et al., 2012) and rotifers (Makarewicz et al., 1995). Zooplankton composition varies also throughout the salinity gradient thus giving rise to diverse population of zooplankton (Jayasinghe et al., 2003; Johan et al., 2012). Abiotic factors such salinity, temperature, pH and nutrients can influence the distribution of zooplankton species (Mageed, 2007; Bozkurt and Guven, 2009; Beaugrand, 2009; Beaugrand et al., 2009; Brucet et al., 2010). It was also, pointed out by several researchers that there is a direct relation between increase in nitrites, nitrates, phosphates and the abundance of zooplankton (rotifers, cladocerans and copepods) (Esler et al., 2001; Vakkilainen et al., 2004). Because of climate change, Mediterranean coastal wetlands may have changes in salinity and a reduction in the time and extent of wetland inundation, due to the increase of marine influence and the rise of temperature and evaporation, respectively (Nielsen and Brock, 2009). These changes will have consequences in species composition and food web interactions (Hughes and Stachowicz, 2004; Fischlin et al., 2007). In zooplankton community, it is expected that these changes will have a great impact, since the increase in salinity and reduction of hydroperiod will lead to a reduction in diversity and to important changes in community composition (Boix et al., 2008; Waterkeyn et al., 2008). On one hand, salinity is known to be a strong mechanism of change in aquatic communities, causing the disappearence of species that cannot tolerate the increase of salt concentration and/or a reduction in species richness and diversity in the zooplankton community (Boix et al., 2008; Nielsen et al., 2008; 2009; Jensen et al., 2010). This fact will be especially important for cladocerans, except for few salinity tolerant species, as *Daphnia magna* (Amsinck et al., 2003; Gonçalves et al., 2007; Ortells et al., 2012). This will cause important shifts in zooplankton communities: from a community dominated by large-sized cladocerans at low salinities, to another dominated by copepods and rotifers (Schallenberg et al., 2003; Jeppesen et al., 2007b; Brucet et al., 2010) at high salinities. The purpose of this study was to investigate changes of zooplankton in the man-made Sfax solar saltern (Tunisia) at different seasons in relation to environmental factors.

THE STUDY SITE

This study was performed in the solar saltern of Sfax (central eastern coast of Tunisia, between 34°39′0.1″ N and 10°42′35″ E). It is an artificial system formed of interconnecting ponds (20–70 cm deep) of different salinity which are extended over an area of about 1500 ha, along the coast to the south of the town of Sfax (Tunisia) over a distance of 12 km (Elloumi et al., 2006) and on a peninsula situated between the port zone and the village of Gargour. The saltern is separated from the sea by a red silt artificial seawall (Figure 1).The input of seawater and the circulation between the various ponds are entirely controlled depending on the meteorological conditions in order to ensure an annual yield of about 300.000 tonnes of halite and 25.000 tonnes of bittern brine.

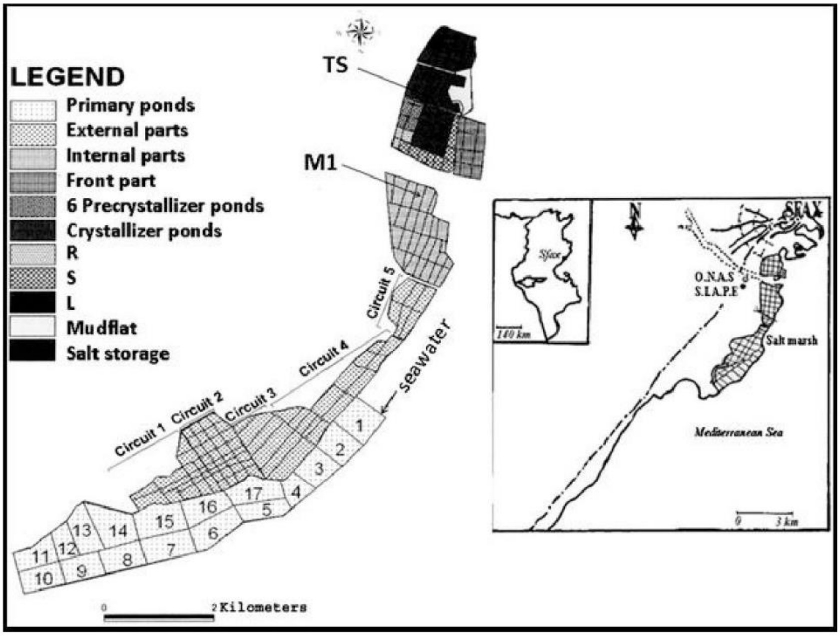

Figure 1. Map of the location of the sampling ponds 1(A1), 5(A5), 16(A16) and 31(C31) of the Sfax Solar Saltern in Tunisia (Amdouni 1990).

MEASUREMENTS OF THE PHYSICOCHEMICAL PARAMETERS

Sampling and monitoring took place, every month, between September 2007 and August 2008. All data were taken in the morning between 07:00 and 11:00 am. Four ponds A1, A5, A16 and C31 (Figure 1) were chosen for sampling in the four ponds of the solar saltern of Sfax whose salinity increased as follows: A1, 41 psu; A5, 46 psu; A16, 67 psu; and C31, 77 psu. Samples for physicochemical and biological analysis were collected at 20 cm below the surface with a 5 l Van Dorn bottle. Water temperature and pH were measured *in situ* using a mercury glass thermometer graduated in 0.1 °C and a Metrohm® type pH meter. Salinity, as totally dissolved salts, were estimated by the dry residue method, which consists of evaporating a 50 ml sample (24 h, 180 °C) in a previously sterilized crystallizing dish (by heating at 550 °C for 1 h), and calculating the salt content from the difference in weight before and after evaporation (Elloumi et al., 2009). Suspended particulate matter concentrations (SM) were measured by filtration through a Whatman GF/C membrane and by determining the residue's dry weight. Samples for nutrient such as dissolved inorganic nitrogen (nitrites: NO_2^-, nitrates: NO_3^-, ammonium: NH_4^+), total phosphorus (TP) and orthophosphates (PO_4^{3-}) were preserved immediately upon collection (-20 °C, in the dark) and analysed within 15 days. Nutrients analyses were performed with an automatic analyser type 3 (Bran & Luebbe) using standard methods (Tréguer and LeCorre, 1975).

MEASUREMENTS OF BIOTIC PARAMETERS

Chlorophyll *a* (Chl *a*) was analyzed spectrophotometrically from samples (0.15 1) collected on Whatman GF/F glass fiber filters (0.45 mm pore size). Chl (*a*) was extracted in 10 ml of 90% acetone and concentrations were calculated according to Strickland and Parsons (1968) equations. To identify and determine the abundance of phytoplankton and ciliates cells, water samples (200 ml), were collected from the surface water using a 5 l Van Dorn bottle, simultaneously with the samples for chemical analysis. Samples were preserved with acid Lugol's iodine (1% final concentration) and stored in the dark at 4 °C until laboratory analysis. An inverted microscope (Leitz) at 400 magnification was used for the enumeration according to the Uthermöhl (1958) method after sedimentation in settling chambers of 10 ml subsamples for at least 3 h. The taxonomic identification was carried out according to the keys of Drebes (1976), Trégouboff and Rose (1978), Dodge (1982), Ricard (1987), Balech (1988) and Tomas et al. (1996). Identification of ciliate species determined in accordance using the keys of Trégouboff and Rose (1978), Foissner and Berger (1996), Petz (1999), Alder (1999) and Strüder-Kypke and Montagnes (2002). Zooplankton samples were collected by filtering 50 l of water at each pond with a plankton net (50 µm mesh size), fixed in situ with neutralized 5% formalin solution and coloured with Bengal rose (Eleutheriou and Moore, 2005). The abundance of different species (>30 pm) of zooplankton was expressed as individuals per litre. The identification of the different zooplankton species was carried out according to Rose (1933), Bradford-Grieve (1999), Dussart (1969), Boxshall and Halsey (2004), Trégouboff and Rose (1978) and Wells (2007). The zooplankton taxa were enumerated and counted in Dolffus chambers under a binocular Leica microscope.

STATISTICAL ANALYSES

The potential relationships between abiotic and biotic variables were tested by Pearson's correlation coefficient. In addition, One-way ANOVA was applied to identify significant differences ($p<0.001$, $p<0.01$, $p<0.05$) between physicochemical and biological parameters between the four ponds. ANOVA tests were made using XL stat software. The data recorded in this study were examined also with a normalized principal component analysis (PCA). Physicochemical variables such as temperature, salinity, suspended matter and nutrient's concentrations and biological parameters (zooplankton, rotifer, cladocereans, other zooplankters, phytoplankton and ciliates) were assessed by examining the projection of the plots of the extracted factors on a factorial plan consisting of the statistically significant axis of the PCA analysis.

THE VARIATION OF THE PHYSICOCHEMICAL PARAMETERS

The results concerning the physicochemical parameters recorded in the four ponds are summarized in Table 1. The salinity varied from 38 psu (April, 2008) to 86.1 psu (December, 2007) in the ponds A1 and C31, respectively (Figure 2.a). The seasonal salinity changes were clear in each pond. The highest values were found in pond C31, with a mean of 77.02±4.39 psu (Table 1). Statistically significant difference in the salinity was found between ponds (ANOVA, F = 129.62; $p<0.001$). In contrast, temperature did not differ significantly among the four ponds (ANOVA, $p>0.05$) (Table 1). The average water temperature ranged between 11.5 and 30 °C (Figure 2.b). The lowest value (11.5 °C) was recorded at the pond A1 on January 2008, while the highest (30 °C) at the pond A16 on September 2007 (Figure 2.b).

Table 1. Environmental parameters (mean±sd) in the ponds A1, A5, A16 and C31 of the Sfax Solar Saltern in Tunisia

Physico-chemical and biological parameters	Ponds				*F values*
	A1	A5	A16	C31	
Physical parameters					
Salinity (p.s.u)	41.54 ±2.38	46.42±5.29	67.63 ±7.28	77.025 ±4.39	129.62***
Suspended matter (µg. l^{-1})	399.37 ±217.83	1285.52 ±1142.66	1130 ±927.85	1383.48 ±571.31	3.75*
Temperature (°C)	20.70 ±5.57	21.17 ±5.55	20.90 ±5.86	21.276.16	2.81
Chemical parameters					
NO_2^- (µmol. l^{-1})	1.3±2.2	0.2±0.2	0.3±0.1	0.6±0.3	2.14
NO_3^- (µmol. l^{-1})	2.3±1.2	6.5±3.7	7.1±5.4	6.8±6.7	2.63
NH_4^+ (µmol. l^{-1})	6.3±5.7	5.2±5.8	5.3±4.5	5.7±7.8	0.08
Total-N (µmol. l^{-1})	16.3±7.7	6.65±11.6	13.2±15.9	17±11.8	1.82
PO_4^{3-} (µmol. l^{-1})	19.1 ±11.9	15.3±5	15.8±11.5	17.5±13.8	0.29
Total-P (µmol. l^{-1})	60.5 ±57.3	9±4.78	8.6±7	14.5±11.2	8.62***
$Si(OH)_4$ (µmol. l^{-1})	12.65 ±13.84	6.22 ±6.66	10.29 ±5.72	12.67 ±10.52	1.16
Biological parameters					
Chlorophyll-*a* (mg. l^{-1})	0.094 ±0.026	0.103 ±0.015	0.11 ±0.028	0.102 ±0.034	10.04***

F-value : between-groups mean square/within –groups mean square. Values in the same row showing the same letters are significantly different as tested with one-way ANOVA ($p<0.05$). *$p<0.05$; **$p<0.01$;***$p<0.001$.

There were similar seasonal variations in all ponds, with peak values in summer (25.16, 25.4, 25.66 and 26.83 °C) and minimum values in winter (13.66, 13.98, 13.87 and 14.11 °C) in the ponds A1, A5, A16 and C31, respectively (Figure 2.b).

Thermal stratification did not establish because of the shallowness of the sampled stations (<1 m). Temperature was correlated negatively with salinity, especially from April to September. This paradox was ought to the opening of water gates by the saltern's managers to feed the ponds with seawater. However, from November 2007 to February 2008, the distribution of salinity in all the ponds did not display neither a clear pattern nor a relationship with temperature, while during March to January 2008 salinity distributed similarly to temperature.

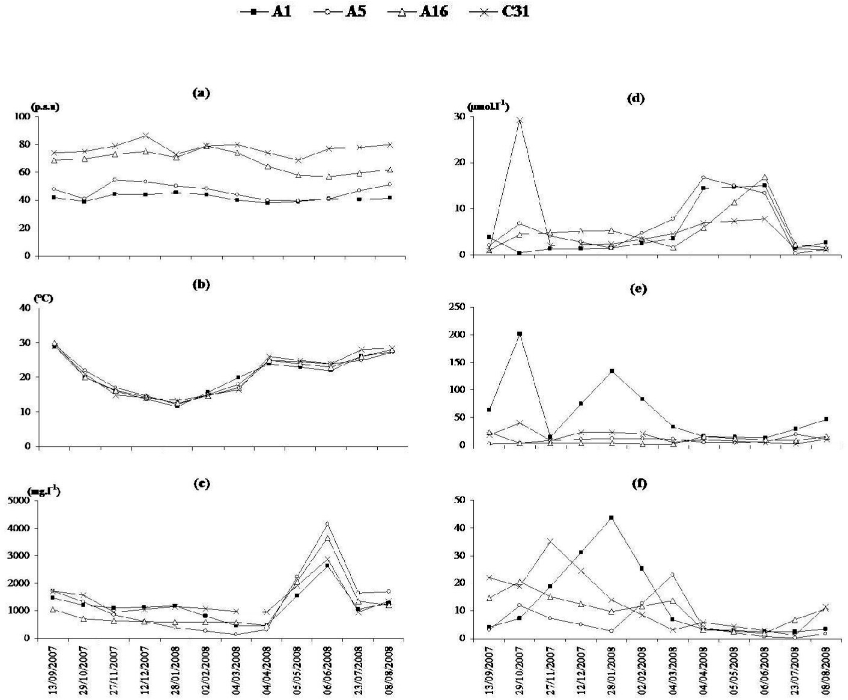

Figure 2. Spatial and temporal variation of physicochemical parameters, (a) salinity, (b) temperature, (c) suspended matter, (d) NH4+, (e) TP and (f) Si(OH)4 in the ponds A1, A5, A16 and C31 of the Sfax Solar Saltern in Tunisia.

Concentrations of suspended matter (SM) ranged between 145 (March 2008, A5) and 4160 $mg.l^{-1}$ (August 11, 2003) (Figure 2.c), rising with increasing temperature ($r=0.382$, $p<0.01$). Differences in suspended matter concentrations between the four ponds were found (ANOVA, $F = 3.75$, $p<0.05$) (Table 1). The pH did not differ significantly among the four ponds (ANOVA, $p<0.05$) and ranged from 6.75 to 9 with a high mean value of 8.20 in the pond A16 (Table 1). In September 2007, higher pH values occurred in the four ponds, but in January 2008 lower pH appeared in the pond C31.

Nutrient concentrations did not differ significantly among the four ponds exept for total phosphorus (ANOVA, $F = 8.62$, $p<0.001$). Ammonium NH_4^+

constituted the most important fraction (59.10% and 43.41%) of the total nitrogen in A5 and A16, respectively. Highest values were recorded in C31 with 29.33 µmol.l^{-1} in October 2007 (mean±sd = 5.78 ±7.83 µmol.l^{-1}) (Figure 2.d). The concentration of TP varied from 1.92 µmol.l^{-1} (March, 2008) and 201.48 µmol.l^{-1} (October, 2007) in the pond A16 and A1, respectively (Figure 2.e). Orthophosphate's concentrations fluctuated from 0.93 µmol.l^{-1} (in C31, July 2008), to 41.08 µmol.l^{-1} (in C31, March 2008). $Si(OH)_4$ varied from 0.19 µmol.l^{-1} (in A5, July 2008) to 43.64 µmol.l^{-1} (in A1, January 2007) (Figure 2.f) (Table 1).

SPATIAL AND TEMPORAL DISTRIBUTION OF PHYTOPLANKTON, CHLOROPHYLL *A* AND CILIATES

Total phytoplankton abundance varied from $57.99\times10^3 \pm 29.98\times10^3$ (A16) to $85.44 \pm 26.58\times10^3$ cells l^{-1} (A5) (Figure 3). The phytoplankton community was composed by diatoms, dinoflagellates, cyanobacteriae, euglenophyceae and silicoflagellates. Diatoms dominated in the phytoplankton community in ponds A1 (63%) and A5 (54%) (salinity <50 psu), while dinoflagellates dominated in ponds A16 (57%) and C31 (63%) (salinity >50 psu) (Figure 3). The lowest average density of total phytoplankton was recorded during winter in pond A1 (29×10^3 cells l^{-1}) and C31 (34×10^3 cells l^{-1}). Concentrations of chlorophyll *a* varied between 0.055 mg.l^{-1} (A1, June 2008) and 0.187 mg.l^{-1} (C31, June 2008), with a mean value of 0.094 ± 0.026 mg.l^{-1} in the pond A1 and increased with increasing of salinity, but showed a negative correlation with the abundance of other zooplankters (Pearson's $r = -0.3$, $p<0.05$) (Figure 5) (Table1). There was a peak of Chl *a* in March 2008 with 0.136 mg.l^{-1} (in pond A1), 0.139 mg.l^{-1} (in pond A5) and 0.162 mg.l^{-1} (in pond A16), while the highest value was recorded in June 2008 at pond C31 with 0.187 mg.l^{-1} (Figure 5).

The abundance of total ciliates fluctuated between 0.5×10^3 cells l^{-1} (pond A1, 4 March) and 186×10^3 cells l^{-1} (pond A5, 21 January). The highest ciliate density was recorded in pond A5 (mean = 36.258×10^3 cells l^{-1}) concomitant with the strong proliferation of the Oligotrichidae group which contributed 87% of total ciliates (Figure 4). Differences between ponds were negligible (ANOVA, $p<0.05$). The abundance of total ciliates decreased with increasing temperature ($r = -0.314$, $n = 20$, $p < 0.05$).

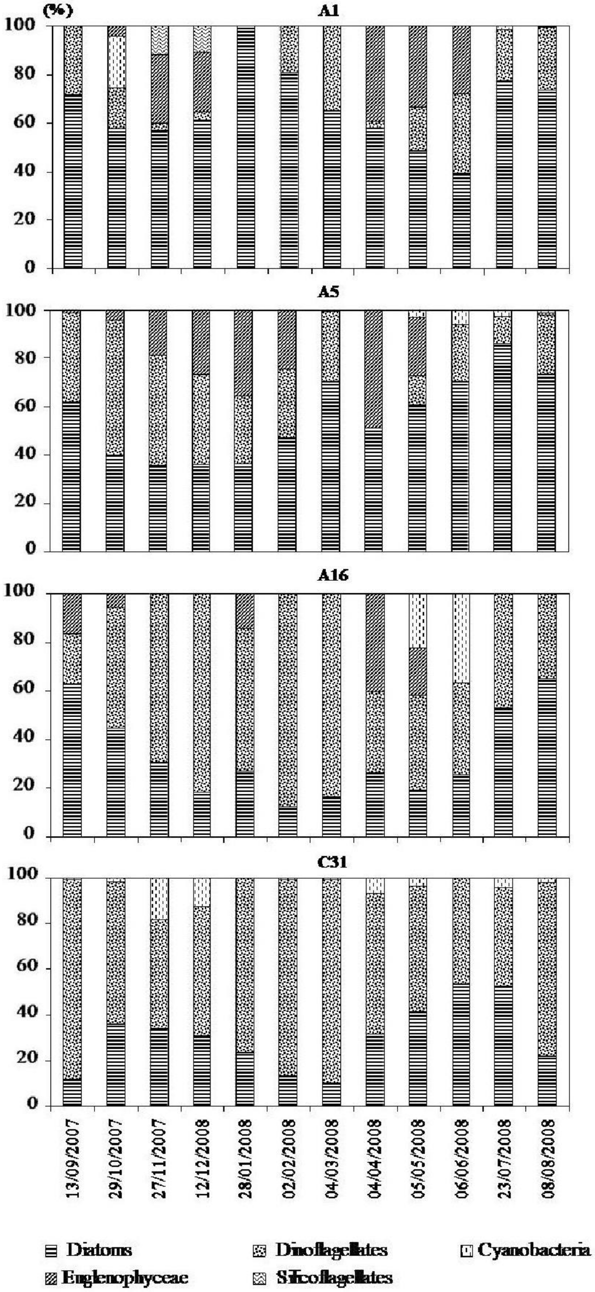

Figure 3. Abundance of phytoplankton groups in the ponds A1, A5, A16 and C31 of the Sfax Solar Saltern in Tunisia.

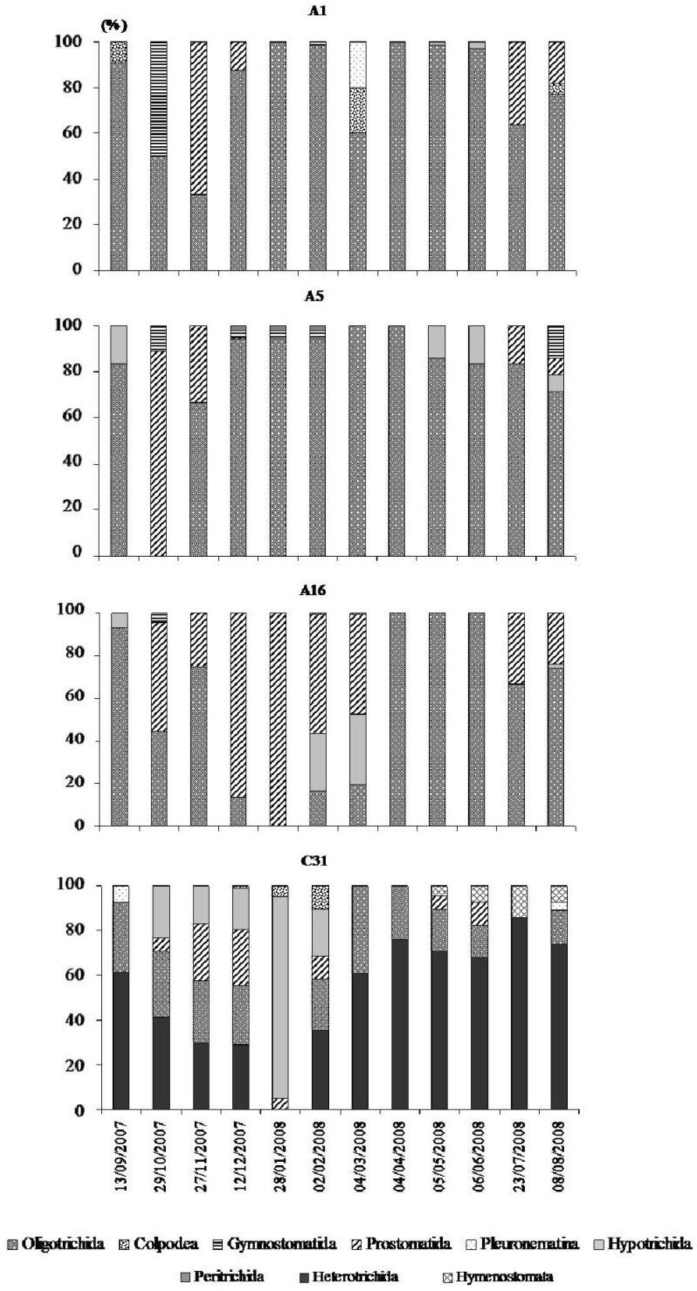

Figure 4. Abundance of ciliate groups in the ponds A1, A5, A16 and C31 of the Sfax Solar Saltern in Tunisia.

SPATIAL AND TEMPORAL DISTRIBUTION OF THE ZOOPLANKTON COMMUNITY

The total zooplankton abundance ranged from 1.89 × 10^4 ind.m^{-3} to 200.175 × 10^4 ind.m^{-3}, and the values exhibited an obvious decreasing trend from the pond A1 to C31 (Figure 5).

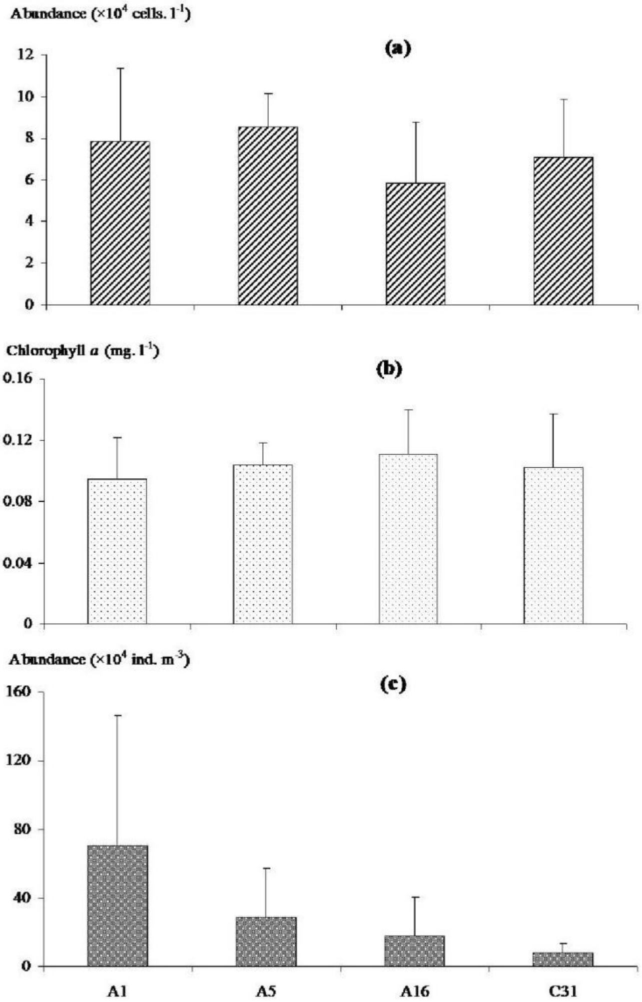

Figure 5. Temporal and spatial variation of average of total phytoplankton abundance (a), chlorophyll *a* concentrations (b) and total zooplankton abundance (c) in the ponds A1, A5, A16 and C31 of the Sfax Solar Saltern in Tunisia.

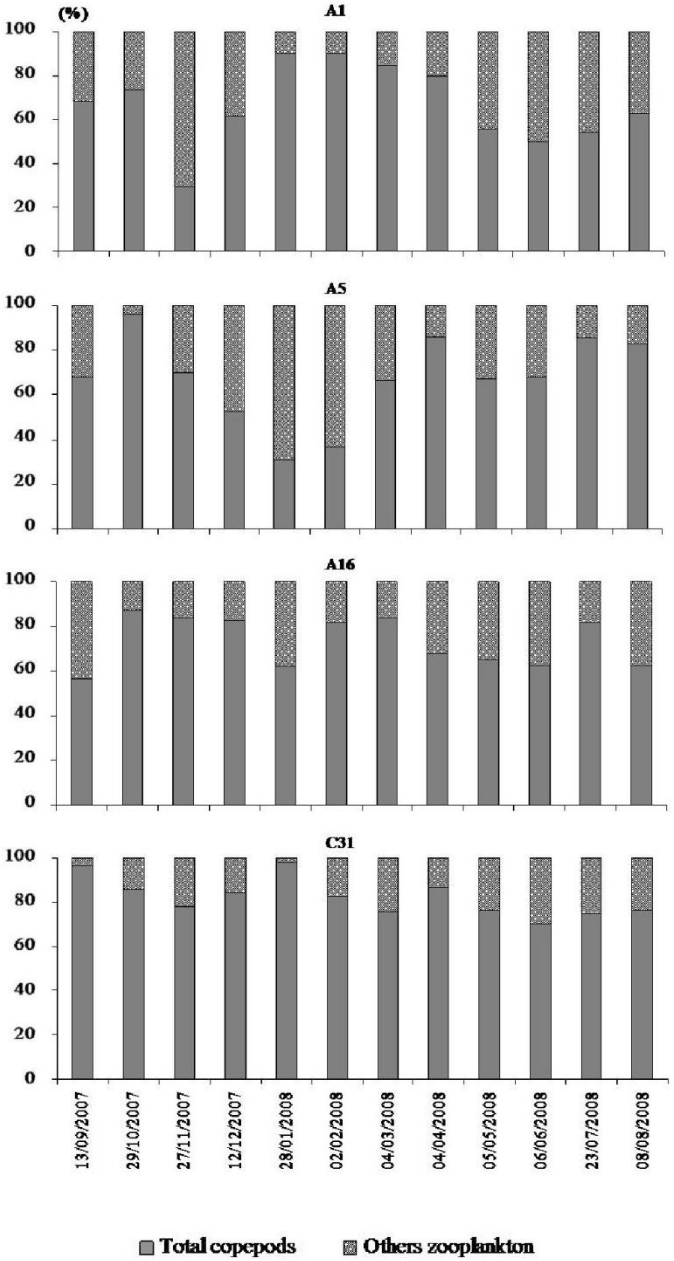

Figure 6. Abundance of zooplankton groups in the pond A1, A5, A16 and C31 of the Sfax Solar Saltern in Tunisia.

In pond A1, the abundance values ranged from 7.494 × 10^4 ind.m^{-3} (April, 2008) to 200.175 × 10^4 ind.m^{-3} (January, 2008) (70.762 ± 75.498 × 10^4 ind.m^{-3}) (Figure 5). The zooplankton community was dominated by copepods (46.452 ± 55.439 × 10^4 ind.m^{-3}), which accounted for more than 65% of the total zooplankton. The dominant species were *Oithona similis* (18 % of the total zooplankton), *Clytemnestra scutellata* (16 %) and *Oithona nana* (14 %), respectively (Figure 6). The rotifers were present occasionally in all the ponds and were dominant in the pond A1, and their abundance ranged between 0.2 × 10^4 ind.m^{-3} and 2 × 10^4 ind.m^{-3} with a mean value of 1.166 ± 0.571 × 10^4 ind.m^{-3}. Cladocerans were only occurred in the pond A1 (41psu) and ranged from 0 to 3040 ind.m^{-3}.

In pond A5, the density of total zooplankton varied between 5.246 × 10^4 ind.m^{-3} (March, 2008) and 102.52 × 10^4 ind.m^{-3} (July, 2008) with a mean value of 28.75 ± 28.50 × 10^4 ind.m^{-3} (Figure 6). Copepods (copepodites and nauplii) were the most abundant group (74.68 % of the total zooplankton), the mean values being 21.474 ± 25.736 × 10^4 ind.m^{-3} (Figure 6). *Oithona nana* and *Bryocamptus* sp. were the dominant species of copepods, accounting for 24 % and 16 % in the total zooplankton, respectively. The density of other zooplankters oscillated between 1.1 × 10^4 ind.m^{-3} (October, 2007) and 16.2 × 10^4 ind.m^{-3} (January, 2008) with a mean value of 6.9 ± 5.55 × 10^4 ind.m^{-3} (24.14% of the total zooplankton) (Figure 6). The total rotifers abundance varied from 0 to 0.8 × 10^4 ind.m^{-3} (mean±sd = 0.316 ± 0.279 × 10^4 ind.m^{-3}). *Brachionus urceolaris* was the only species recorded in this pond.

In pond A16, the total zooplankton abundance varied between 1.89 × 10^4 ind.m^{-3} (January, 2007) and 76.9 × 10^4 ind.m^{-3} (September, 2007) (mean±sd = 17.582 ± 23.257 × 10^4 ind.m^{-3}) (Figure 5). The copepods dominated the zooplankton community (68 % of the total zooplankton) (mean±sd = 11.866 ± 13.563 × 10^4 ind.m^{-3}) while the remaining groups accounted for 31.47 % (mean±sd = 5.53 ± 9.87 × 10^4 ind.m^{-3}) (Figure 6). The dominant species were *Brachionus urceolaris* and *Brachionus plicatilis* ((82 % and 18 % of total rotifers). In pond C31, total zooplankton density assorted from 2.64 × 10^4 ind.m^{-3} (January, 2008) to 21.625 × 10^4 ind.m^{-3} (July, 2008) (mean±sd = 8.09 ± 5.46 × 10^4 ind.m^{-3}) (Figure 5). The zooplankton community was dominated by copepods (6.45 ± 4.07 × 10^4 ind.m^{-3}), which accounted for 79.75 %, while the other groups accounted for 19.83 % (1.59 ± 1.49 × 10^4 ind.m^{-3}) (Figure 6). Rotifers reached a low density which ranged between 0 and 0.2 × 10^4 ind.m^{-3}. Differences in the density of total zooplankton and copepods were found between ponds (ANOVA, F = 5.17, $p<0.01$) and (ANOVA, F = 3.82, $p<0.05$), respectively.

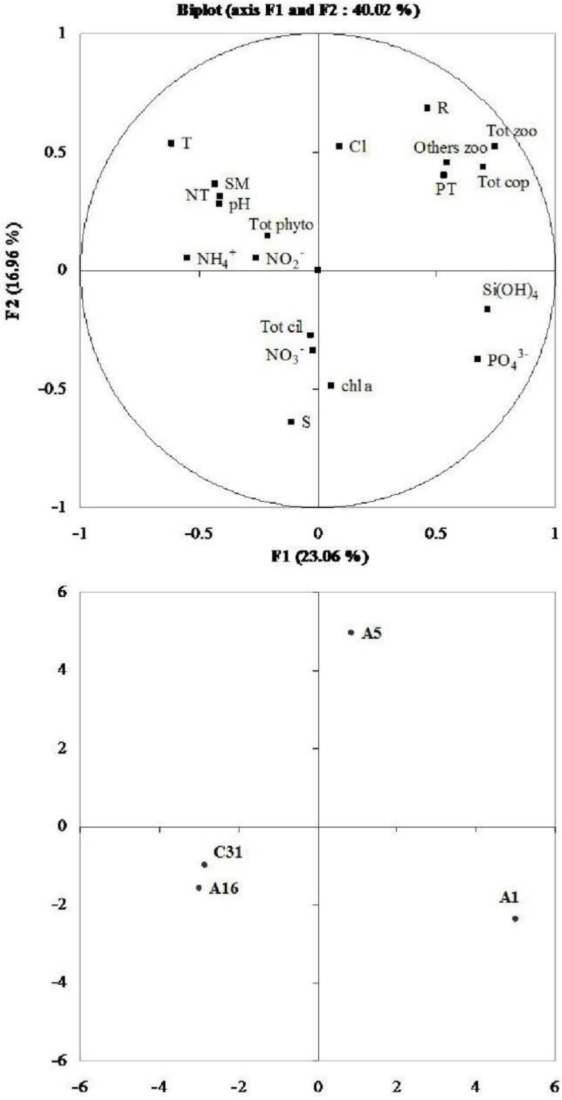

Figure 7. PCA performed on biological parameters and different environmental factors in four ponds during 1 year of study. Axis1 and 2 biplot for species and environmental variables. Water temperature (T), salinity (S), suspended matter (SM), pH, nitrates (NO^{-}_{3}), ammonium (NH_4^+), total nitrogen (TN), total phosphorus (TP), orthophosphates (PO_4^{3-}), total phytoplankton (Phyto tot), chlorophyll a (Chl a), total ciliates density (tot cil), total zooplankton density (tot zoo), total copepods density (tot cop), total rotifers density (R), total cladocerans density (Cl), other zooplankters density (others zoo). All dates included. A1, A5, A16 and C31: ponds.

PRINCIPAL COMPONENT ANALYSIS

A principal component analysis (PCA) was used to explore the relationships between environment variables, phytoplankton, ciliates and zooplankton composition as shown in Figure 7. The principal component analysis (first plot) allowed two groups to be discriminated around the F1 and F2 axes. Axis F1, which represents 40.02 % of the variability, positively selects group G1, which is composed of the total zooplankton, along with copepods, rotifers, cladocerans, other zooplankters, as well as abiotic factors such as total phosphorus (TP) and silicates, while negatively selects the salinity and the orthophosphates PO_4^{3-}. PCA suggests that the zooplankton distribution was influenced by salinity ($r = -0.355$, $n = 12$, $p = 0.05$) (Figure 7). Axis F2 explains 16.96 % of the variability and positively selects group G2 formed by total phytoplankton, temperature, suspended matter, pH and ammonium NH_4^+ (Figure 7).

THE EFFECTS OF ENVIRONMENTAL PARAMETERS TO THE ZOOPLANKTON VARIABILITY

Different studies carried out in Mediterranean wetlands found that salinity and water permanence were the main environmental gradients causing the spatial heterogeneity (Brock et al., 2005; Boix et al., 2008; Waterkeyn et al., 2008; Anton-Pardo and Armengol, 2010). An extensive literature exists showing the associations between local environmental variations and the structure of zooplankton communities (Schell et al., 2001; Hobaek et al., 2002), as well as the influence of human activities on these communities (Dodson and Lillie, 2001; Dodson et al., 2005; Angeler & Moreno, 2007; Dodson et al., 2007). The zooplankton community in the solar saltern of Sfax was dominated by copepods, being in agreement with the study of Magalhăes et al. (2010). Copepods are among the mainly secondary producers (Islam et al., 2006), playing a relevant role in nutrient recycling and in the transfer of energy between phytoplankton and bacterioplankton to the highest trophic levels (Magalhães et al., 2010; 2011). Moreover, the salinity gradient has been found to be one of the main factors influencing the distribution of pelagic and benthic animals (Nérot, 2011). In the Sfax solar saltern there was negative correlations between salinity and the density of the total zoopankton, as well as copepods and rotifers. Similar results were found by Britton & Johnson

(1987) on the Salins de Giraud, where a strong decrease in the number of invertebrate species with increasing salinity was noted. A study conducted on a saltern in the Camargue, also emphasized the importance of the salt concentration but also of the temperature in the regulation of zooplankton abundance (Thiéry and Puente, 2002).

Zooplankton species succession and spatial distribution result from differences in ecological tolerance to abiotic and biotic environmental factors (Beaugrand et al., 2002; Pedrozo and Rocha, 2005; Voarino, 2006; Ahmet and Suleyman, 2009). The principal component analysis confirmed the negative effect of salinity on total zooplankton, being in agreement with other published studies (Jayasinghe et al., 2003; Magalhăes et al., 2010; Johan et al., 2012). Also, a negative correlation was recorded between copepods and salinity. Similar observations were reported by others (Frisch and Green, 2007; Krumme and Liang, 2004; Ara, 2004; Osore et al., 2003; Mwaluma et al., 2003; Madhu et al., 2007). Our results showed a negative correlation between salinity values and rotifer abundance, although several studies have reported the positive impact of salinity on rotifer’s distribution (Park and Marshall, 2000 a; Isabelle et al., 2005). The dominance of one genera, namely *Brachionus*, has been regularly reported in shallow environments (Green, 2003; Castro et al., 2005) and it was attributed to the fact that these organisms are r strategists, or opportunists, with short life cycles and wide tolerance to a variety of environmental factors (Neves et al., 2003; Sellami et al., 2009). Besides salinity, the present results indicate that other environmental elements, such as temperature, are the dominant factors which explain the ordination of crustacean taxa, and they were considered to be important in influencing the dynamics and composition of zooplankton in solar salterns (Alheit et al., 2005; Möllmann et al., 2006; Möllmann et al., 2008; Hansson et al., 2010). In this sense, highly negative correlation was recorded between temperature and abundance of total zooplankton and copepods,in the pond A1, although a positive correlation was recorded between temperature and abundance of total zooplankton, copepods and other zooplankters in the pond A16. Similar results have been reported by (Beaugrand and Ibanez, 2004; Devreker et al., 2008).

The increase of temperature, salinity and the decrease of the water quality, have negative effects in the populations and species richness, while these parameters seems to have little affection to rotifers which are more tolerant than small copepods (Hansson et al., 2007). The predominant zooplankton groups in all the ponds of the solar saltern of Sfax and in all dates, were copepods and in some cases other zooplankters such as the larvae of annelid polychaetes. An inverse relationship between cladocera, ostracoda, copepoda, rotifera and salinity was observed, and the population density of arthropoda and rotifera as well as cladocera, copepoda and ostracoda was related to the abiotic factors mainly the salinity. In fact, for some groups, increasing salinity values were a major density-controlling factor (Toumi et al., 2005; Toumi, 2006). This significant effect was also observed with the other zooplankton groups which was composed mainly of larval forms of annelids and crustacea, which only occurred sporadically in the ponds with salinity greater than 40 psu (Toumi et al., 2005; Toumi, 2006).

In the present investigation, there was no significant correlation between the zooplankton community and the suspended matter which is in accordance to Bouillon et al. (2000; 2004) who suggested that despite the large amounts of terrestrial and mangrove detritus present in the water column, the locally produced phytoplankton appears to be a more important carbon source for the zooplankton. Nutrient concentrations, particularly phosphates and silicates, in all the ponds of solar saltern in Sfax exhibit similar profiles to those of temperature, however, they excersized an opposite affection to the zooplankton. Indeed, our results indicate that there was a positive correlation between total phosphorus and the abundance of rotifers, copepods and total zooplankton abundance. Nutrient recycling can considerably vary with the composition of the zooplankton community, and existing evidence suggests that rotifers usually have higher rates of phosphorus excretion per unit of biomass relative to copepods (Ejsmont-Karabin et al., 2004; Kowalezewska-Madura et al., 2007; Teubner et al., 2003). Several studies have also showed that zooplankton communities were correlated to nutrients (Weider et al., 2004; Pinto-Coelho et al., 2005; Badosa et al., 2006), which may partly determine the species presence and dynamics of rotifer assemblages (Sukumaran and Das, 2004; Toumi et al., 2005; Toumi, 2006; Drira, 2009).

The principal component analysis confirmed the effect of Chl *a* and phytoplankton on the zooplankton density. In fact, in ponds A5 and A16, negative correlation was recorded between Chl *a* concentration and abundance of total zooplankton and copepods, while this was also the fact for other zooplankters (in pond A16). Similar results have been reported (Striebel et al., 2008; Perhar and Arhonditsis, 2009; Brett et al., 2009). Thus, we infer that the food resources represented by phytoplankton and ciliates, may also be an important driver of zooplankton community structure in the saltern. Most studies carried out along the coast of Sfax (Drira et al., 2010; Rekik et al., 2012) and in other marine systems (Rollwagen-Bollens et al., 2011) found that the quantity and quality of specific types of food would be expected to affect variation in zooplankton composition.

The present results revealed that pH having the least variation did not exert any significant correlation with the total zooplankton density, similar to other observations (Ahmadi et al., 2005). However, the density of cladocerans could be positively related to pH and acidity, as it was also reported by Okogwu (2009). On the other hand, the peak of cladocerans in autumn 2007 resulted probably from the entry into competition with rotifers. Similar observations were reported by other investigators (Paranaguá and al., 2005; Yarwood-Buchanan, 2005) and with other zooplankters. Thus, the results are in agreement with other published studies dealing with the distribution of zooplankton (Tillmann et al., 2008). According to various studies (Duggan et al., 2001; Mageed, 2007) rotifers are usually considered to be useful indicators of water quality and the trophic status of aquatic ecosystems (Whitman et al., 2004; Baião and Boavida, 2005; Drira, 2009) and, thus, the presence of the genus *Brachionus* is indicative of moderate to high organic pollution (Mola, 2011). Determining the current trophic state of solar saltern in Sfax based on the analyzed variables and with the available data and models is complex. The chlorophyll *a* concentrations were very low (Table 1), although slightly higher in A16 than in the other ponds. Similar observations were reported by (Toumi et al., 2005). According to the OECD (1982), the high phosphorus levels recorded especially in the pond A1, the saltern could also be classified as eutrophic system, which can be attributed to anthropogenic interference in the Sfax coastal waters (Elloumi et al., 2008; Khemakhem et al., 2010; Rekik et al., 2012; Kobbi-Rebai et al., 2012).

CONCLUSION

In conclusion, spatial and temporal variations in zooplankton throughout the ponds A1, A5, A16 and C31 of the Sfax Solar Saltern in Tunisia can be related to variations in the environmental variability, while salinity seems to play a major role in determining spatial and temporal patterns of total zooplankton distribution and abundance.

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