J. Limnol., 2014; 73(3): 536-550
DOI: 10.4081/jlimnol.2014.958

ORIGINAL ARTICLE

Phytoplankton functional groups for ecological assessment in young sub-tropical reservoirs: case study of the Nam-Theun 2 Reservoir, Laos, South-East Asia

Joanna MARTINET,[1] Stéphane DESCLOUX,[2] Pierre GUEDANT,[1] Frédéric RIMET[3*]

[1]Nam Theun 2 Power Company Limited (NTPC), Environment & Social Division - Water Quality and Biodiversity Dept., AE Lab, Gnommalath Office, PO Box 5862, Vientiane, Laos; [2]EDF, Hydro Engineering Centre, Savoie Technolac, 73373 Le Bourget du Lac, France; [3]Institut National pour la Recherche en Agriculture (INRA), UMR Carrtel, 75 av. de Corzent, BP 511, 74203 Thonon les Bains Cedex, France

*Corresponding author: frederic.rimet@thonon.inra.fr

ABSTRACT
The early stages following the creation of reservoirs are typically physical and biological unstable periods due to the conversion from a lotic to a lentic ecosystem. The sub-tropical Nam Theun 2 Reservoir (Laos) was impounded in 2008. Several limnological parameters were monitored from March 2009 to December 2011 in order to understand the evolution of the phytoplankton community. A strong inter annual variability of hydrodynamic pattern was observed. Rainfall and hydraulic balance were the main physical factors driving the community structure. Periods of highest hydraulic stability led to a phytoplankton biomasses increase. The first assemblages were dominated by the S-C-strategists reaching high biomasses but low diversity. Over the three years, phytoplankton became more diverse due to a diversification of ecological niches, mostly explained by a greater water transparency and a more stable thermal stratification. The applicability of functional groups for biomonitoring in this young sub-tropical reservoir was investigated and compared to a classical taxonomical approach. The dominant functional groups (Lo, A, E, F, N and P) characterized the NT2 Reservoir as meso-oligotrophic with a tolerance to low nutrients supply. Our results support the hypothesis that a functional group approach is more informative than a species-based approach to assess trophic level and dissolved organic carbon concentrations in such reservoirs

Key words: Phytoplankton biomass, functional groups succession, young sub-tropical reservoir, trophic level.

Received: January 2014. Accepted: April 2014.

INTRODUCTION

The conversion from a lotic to a lentic ecosystem through the creation of a reservoir affects aquatic community composition and specifically phytoplankton assemblages. As primary trophic resources, phytoplanktonic population kinetics describe an important part of energy transfer known to influence productivity and the whole food web (Prygiel and Haury, 2006). For this reason, investigations on this community are considered as basic tools to understand the ecology of aquatic ecosystems and assess the ecological status of a water body (Buzzi *et al*., 2007; Kaiblinger *et al*., 2009; Wolfram *et al*., 2009; Hu *et al*., 2013). In the recent decades large efforts have been devoted to gain knowledge in phytoplankton interactions with its surrounding environment, especially in temperate lakes (Schindler, 1978). However, it is obvious that existing data and studies on trophic structure are less numerous in tropical than in temperate ecosystems (Jeppesen *et al*., 1999). Studies on phytoplankton structures and dynamics are therefore fundamental in South Asia, where many reservoirs were constructed in the last 10 years and where the potential of their construction is still high.

Phytoplankton communities in lakes and reservoirs depend on several interactions among chemical, physical and biological factors (Lund, 1965). Reservoirs usually contain a wide array of nutrients which concentrations directly influence phytoplankton biomass and especially green algae (Happey-Wood, 1988). Light, nitrogen (N) and/or phosphorus (P) are often considered as limiting factors (Dillon and Rigler, 1974; Vollenweider and Kerekes, 1980; Coley *et al*., 1985; Tilzer, 1990). In tropical areas, phytoplankton growth is mostly regulated by the temperature and rainfalls at the seasonal scale (Talling, 2001; Schagerl and Oduor, 2008). Water column stability leading to stratification period also tends to be an important variable stimulating, for instance, green algae growth in the African Lake Tanganyika (Descy *et al*., 2010). Such factors are themselves functions of the climate and hydrological regimes, the size of the watershed, reservoir basin morphology, volume of outflow, and the food-web structure (Thornthon *et al*., 1990; Calijuri and Dos Santos, 2001). In some Brazilian reservoirs, it has been revealed that climate, hydrology and retention time were major forcing functions which had a strong effect on phytoplankton and in their succession of communities (Tundisi *et al*., 2008).

Initially, Grime (1979) stated that pooling the species sharing similar ecological characteristics into functional groups is more useful for ecological studies than using taxonomic groups. According to this approach, finding explanations on the coexistence of certain phytoplankters with certain water bodies coupled with environmental constraints became a challenge (Krienits *et al*., 1996; Anneville *et al*., 2002; Crossetti and Bicudo, 2005; Descy *et al*., 2010). More recently, Finlay and Esteban (2001) asked the following question: *why do the species live where they do*? Beyond that, several studies emphasize the concept of functional classification on their studies to describe phytoplankton patterns in various aquatic ecosystems (Reynolds *et al*., 2002; Mieleitner *et al*., 2008; Padisák *et al*., 2009; Kruk *et al*., 2010). Most studies on the applicability of phytoplankton functional groups have been conducted in the temperate climate and their use in the study of tropical reservoirs is even less common (Xiao *et al*., 2011; Hu *et al*., 2013), especially in South-East Asia.

Reservoir impoundment modifies key ecological factors by establishing a man-made ecosystem which could dramatically alter its physical, chemical and biological properties. Indeed, the large-scale reservoir constructions had sometimes shown adverse effects in the past, leading to temporary anoxic conditions, eutrophication (Richard *et al*., 1997; Sabater *et al*., 2008) and to the development of toxic algal blooms (Mastin *et al*., 2002). Understanding the major factors structuring phytoplankton communities is thus *essential*, particularly in young sub-tropical reservoirs and during the early stages following the impoundment. The present study aims at evaluating the phytoplankton community responses to environmental disturbances in a newly impounded sub-tropical reservoir in South-Asia: the Nam Theun 2 (NT2) Reservoir. It is expected that functional groups classification actually offers an interesting tool for i) the ecological assessment at the interannual scale; and ii) for understanding phytoplankton colonization of the reservoir. We also evaluated the benefit of using functional groups compared to a species approach in a young sub-tropical environment. Data from the phytoplankton monitoring program of the NT2 Reservoir carried out from March 2009 to December 2011 were used to address these objectives.

METHODS

Study area

The studied system is the NT2 hydroelectric Reservoir located on the Nakai Plateau (Khammouan Province) in Laos (Fig. 1a). The NT2 Reservoir (Fig. 1b) is defined as a shallow monomictic sub-tropical Reservoir (Chanudet *et al*., 2012). The catchment area covers a surface of about 489 km^2 and the reservoir maximum depth is 38 m (average depth of 11 m) leading to a total volume of 3.9 km^3 (EDF-DTG, 2012). The reservoir was impounded between May 2008 and February 2009 (Fig. 2) and the power station was commissioned in March 2010. From the beginning of the hydroelectric production period, the reservoir levels vary between 529.30 and 538.06 m above sea level.

Local climate

The sub-tropical climate is characterized by a monsoon regime, with an average rainfall of 2640 mm per year; the temperature and precipitation patterns define three distinctive seasons (Boonsoong *et al*., 2008; Jung *et al*., 2008). The warm dry season occurs from March to May. The wet season runs from June to October when 80% of annual precipitation occur and lead to an important natural seasonal disturbance of the water body (Chanudet *et al*., 2012). The hottest month is June with an average surface water temperature of 29°C. The cool dry season runs from November to February when the water temperature is decreasing. January is the coldest month with an average surface water temperature of 19.8°C.

Sampling protocol and analyses

Physical, chemical and phytoplanktonic parameters were routinely measured on a monthly basis from March 2009 to the end of 2011 at the Dam site location (RES1 at 50 m from the Dam, Fig. 1b).

A multi-parameters probe (Quanta, Hydrolab) was used to measure physical and chemical variables (*e.g*., water temperature, dissolved oxygen and saturation, pH and conductivity) at the sampling site in the field. Variables were measured every 0.5 m within the five first metres of the uppermost and 1 m below to describe vertical profiles. In addition, precipitations and hydrological variables were monitored. The water level of the reservoir and the dam outflows were given by the probes deployed at the dam structure. The environmental flow is picked up from the water surface while flood are evacuated using flap gates and radial gates. In that case, the water is spilled from a layer of about 8m from the surface water. The water renewal time were calculated from the reservoir volume and the difference between the outflows and the inflows. Water samples for chemistry analyses, determination of the phytoplankton species and biomass were collected in the euphotic zone defined by Secchi disk depth at the sampling site. The sampling strategy follows an integrated method with 1 L of water collected with a Niskin bottle at 5 equidistant depths from the surface to the bottom of the euphotic layer (x 2.5 Secchi depth as recommended by Poikane, 2009). From the 5 mixed litres, 1 L was collected for Chlorophyll (a) analysis by spectrophotometry (APHA standards, 1995), 500 mL were collected and immediately preserved with a Lugol's solution (Vollenweider, 1969) for phytoplankton investigations, and 250 mL were collected for chemistry analyses. Measurements were carried out according to American Standards for water quality (APHA, 1995). Total organic carbon (TOC) and dissolved organic carbon (DOC) were analyzed with IR Spectrophotometry after acidification and combustion. For the total suspended solids (TSS), gravimetry was used after filtration at 1.2 µm and drying 2 h at 103-105°C. Total nitrogen (TN) and total phosphorous (TP) were analyzed by spectrophotometry.

At the laboratory, phytoplankton identification and counting were carried out under inverted microscope (objective x40) with sedimentation chambers (Utermöhl, 1958) following the European standard (NF EN 15204). The transect method (diameter) was adopted. Phytoplankton biomass was calculated using cells biovolume and carbon content of each class assuming that the density of the organisms equals that of water (Wetzel and Likens, 2000). Identifications were based on specialized taxonomic literature (Starmach, 1972, 1974, 1983; Bourrelly, 1981, 1985, 1990; Hindák, 1984, 1988, 1990). The functional group classification proposed by Reynolds *et al*. (2002) and Padisák *et al*. (2009) was used for this purpose.

Statistical methods

Diversity index

Using the formula from Shannon-Weaver, the diversity index (H) is calculated for species and functional groups (Shannon and Weaver, 1949).

Multi response permutation procedure

Multi response permutation procedures (MRPPs; Biondini *et al*., 1985) were computed with the PcOrd software (McCune and Mefford, 2006) to assess the structuring effect of nine variables on phytoplankton communities. These variables were expressed as classes as given in Tab. 1. This analysis calculates an A-statistic, which is a descriptor of within-group homogeneity. This statistic varies between -1 and 1: if the A-statistic approaches 1, the groups are completely different; if the A-statistic approaches 0, the heterogeneity within groups equals what would be expected by chance; if the A-statistic approaches -1 the groups are homogeneous. A P-value is associated to the A-statistic.

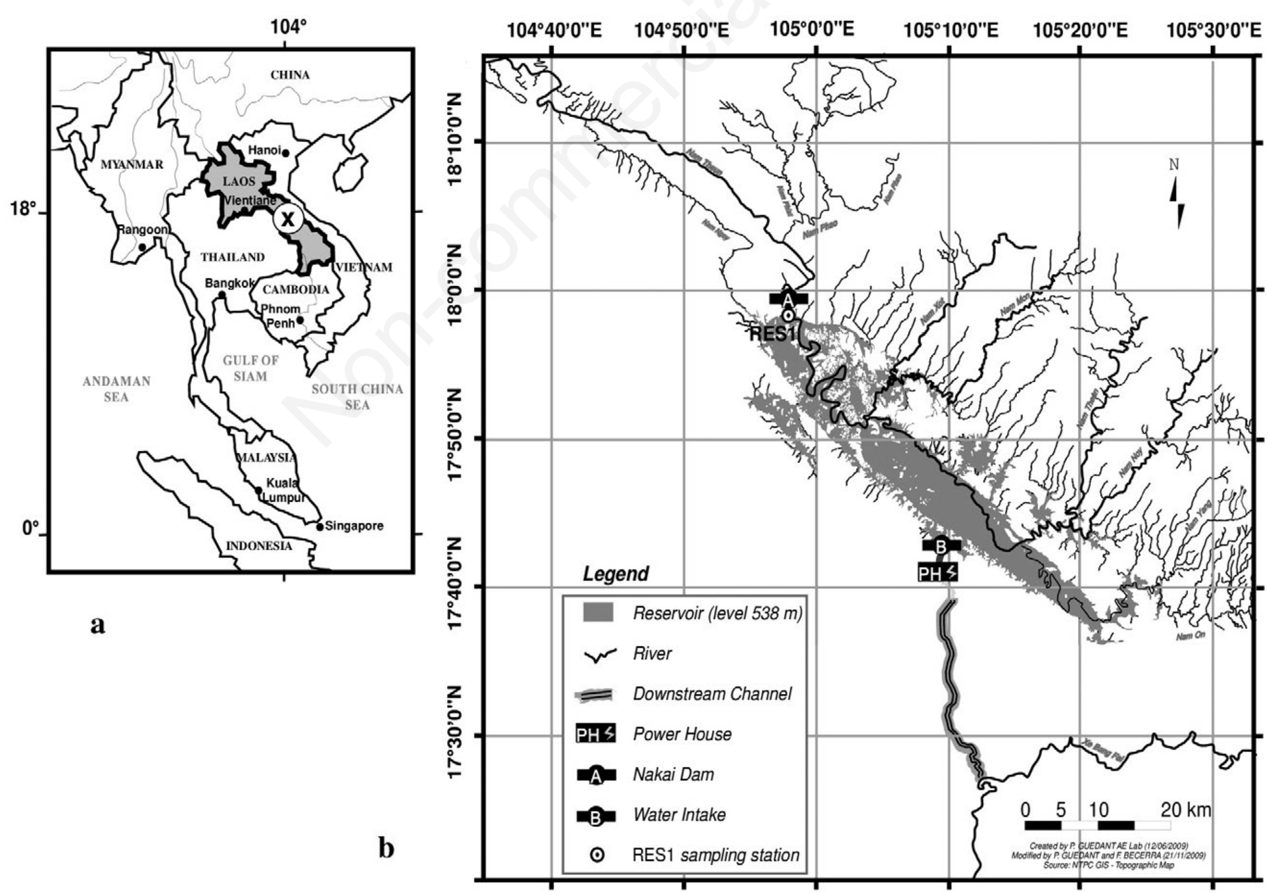

Fig. 1. a) Map of South East Asia with the location of the Nam Theun 2 Reservoir in Laos. b) Map of the NT2 Reservoir and of the sampling site RES1 (Latitude 17°59'51.01''N Longitude 104°57'9.96''E).

Indicator species analysis

Indicator taxa were identified for classes defined for the parameters listed above (seasons, years, pH, TP, TN, DOC, water level, Dam outflows) using the indicator species analysis of Dufrêne and Legendre (1997). This analysis indicates the taxa that are most associated with each pre-defined group. It yields an index calculated on the basis of the abundance and the fidelity of each taxa in each group. If a taxon has a high index in a group, it will be a good indicator of this group. Moreover, this index is tested by means of a Monte-Carlo test; the indices presenting a significant P value (<0.05) are shown for the corresponding taxa. This analysis was computed with the PcOrd software (McCune and Mefford, 2006).

RESULTS

Hydraulic patterns

Over 2009, the reservoir reached its maximum and stable level (538m asl) (Fig. 2). From March 2010, with the starting of the turbines and water intake, the reservoir level fluctuated within the year with the appearance of a drawdown area during the warm dry season followed by a fulfilled period during the wet season (June to October) (Fig. 2). Generally, during the wet season, behind strong rainfalls, water was spilled from the Dam site in order not to exceed reservoir maximum level of 538 m asl. Thereby, the highest renewal of water was reached in June 2011 with 74% of the water renewed during the month whereas the lowest renewal of water was early 2010 with less than 4% of water renewed during February (Fig. 3a).

Physical and chemical results

Generally, the highest total phosphorous and total nitrogen concentrations were measured just after impoundment in 2009. Afterwards (from 2010), only total nitrogen was detectable. After the impoundment period, the highest concentrations were observed in the beginning of the warm-dry season to the end of the wet season, with maximal total nitrogen concentrations occurring for such period (360 μg L^{-1} - 930 μg L^{-1}) (Tab. 2). Even pH was slightly acid over the study, an increase of pH was noticed during the stratification period.

Phytoplankton results

Overview of the phytoplankton composition

A total of 177 taxa were identified in the 34 samples collected over this study. Two classes were fairly involved in biomass dynamic: Chlorophyta and Dinoflagellates. A variety of chlorophyte taxa (including filamentous and desmids) represented more than 80% of the relative abundances – *e.g., Chlorella vulgaris* Beyerinck (Beijerinck), *Monoraphidium* spp. Komárková-Legnerová, *Ankistrodesmus* spp. Corda, *Tetraedron caudatum* (Corda) Hansgrig, *Tetrastrum komarekii* Hindák, *Oocystis parva* West & G.S. West and *Sphaerocystis planctonica* (Korshikov) Bourrelly. They were associated with some Dinoflagellates which comprised up to 94% of total biomasses (mainly species belonging to *Peridinium* spp. Ehrenberg and *Gymnodynium* spp. Stein). Other classes had much lower biomass commonly reaching 10% of total biomasses: Chrysophyceae (Dinobryon genus Ehrenberg with some *Mallomonas* spp. Perty and *Kephyrion* spp. Pascher), Cryptophyceae (*Cryptomonas* spp. Ehrenberg and *Rhodomonas* spp. Karsten), Cyanophyceae (*Aphanocapsa* spp. Nägeli, *Limnothrix redekei* Meffert and *Merismopedia tenuissima* Lemmermann) and Diatoms (*Cyclotella* sp. Kützing, *Eunotia* sp. Ehrenberg and *Rhizosolenia* sp. Brightwell).

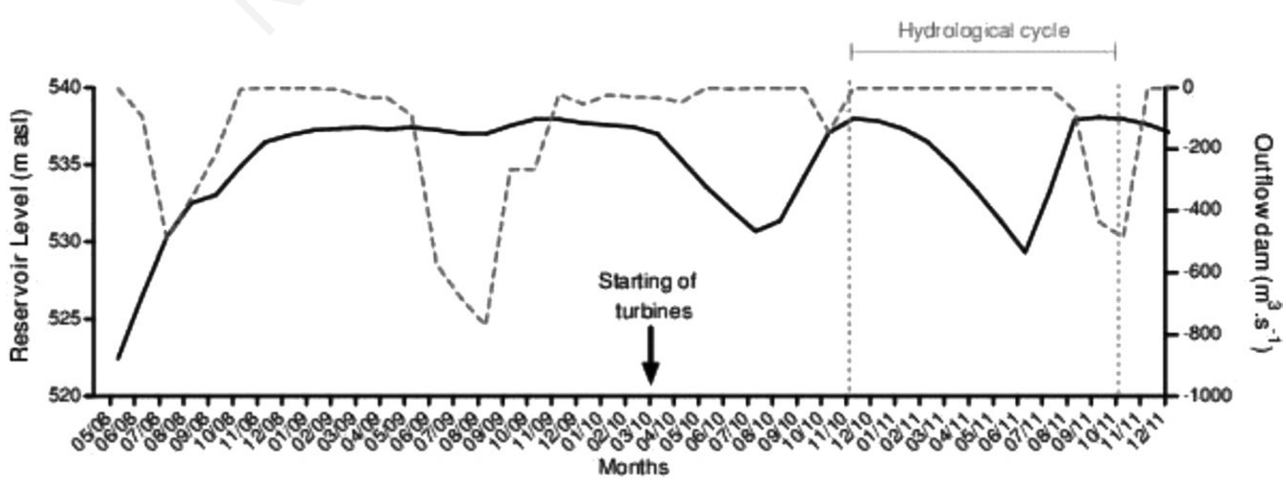

Fig. 2. Graph of hydrological data illustrating the reservoir water level and the outflow from the dam. On the left axis, solid black line corresponds to the reservoir level (m above sea level). On the right axis, dash grey line corresponds to the outflow from the dam site (m^3 s^{-1}).

Dynamics of species and functional groups diversity

Species and functional groups diversities tended to increase over the study period, despite seasonal fluctuations (Fig. 4). Shannon index (H) for species fluctuated from 0.27 in March 2009 up to values reaching approximately 3 in December 2011 (Fig. 4). Similarly, Shannon index for functional groups fluctuated from 0.23 in March 2009 to 1.9 in December 2011 (Fig. 4). Both species and functional group diversity were lower during the wet season, whereas the highest diversity was observed during the warm dry season.

Tab. 1. Parameters expressed as class for the Multi response permutation procedures analyses.

Parameter	Class	Number of samples
Year	Class 1: 2009	10
	Class 2: 2010	12
	Class 3: 2011	12
Seasons	Class 1: cool dry	10
	Class 2: warm dry	9
	Class 3: wet	15
Month	Class 1: January	2
	Class 2: February	2
	Class 3: March	3
	Class 4: April	3
	Class 5: May	3
	Class 6: June	3
	Class 7: July	3
	Class 8: August	3
	Class 9: September	3
	Class 10: October	3
	Class 11: November	3
	Class 12: December	3
pH	$5 \leq$ class 1 < 6	5
	$6 \leq$ class 2 < 6.5	7
	$6.5 \leq$ class 3 < 7	17
	$7 \leq$ class 4 and more	5
Ptot	(mg P L^{-1}) Class 1 < 0.01	24
	$0{,}01 \leq$ class 2 $< 0{,}025$	3
	$0{,}025 \leq$ class 3 $< 0{,}05$	4
	$4 \leq$ class 4	3
Ntot (mg N L^{-1})	Class 1 < 0	9
	$0{,}01 \leq$ class 2 $< 0{,}5$	8
	$0{,}5 \leq$ class 3 $< 0{,}8$	8
	$0{,}8 \leq$ class 4	9
DOC (mg C L^{-1})	$0 <$ class 1 <1	5
	$1 \leq$ class 2 < 2	7
	$2 \leq$ class 3 < 3	12
	$3 \leq$ class 4	10
Water level variation (m)	$- 2.05 <$ class 3 $\leq - 1$	12
	$-1 <$ class 2 $\leq - 0.3$	4
	$-0.3<$ class 1 ≤ 0.15	9
	$0.15<$ class 4 ≤ 1	5
	$1<$ class 5 < 5	4
Dam output (m^3 s^{-1})	class 1 ≤ 63.5	15
	$63.5 <$class 2 ≤ 2305	10
	$2305 <$ class 3 ≤ 15100	6
	$15100 <$ class 4	3

DOC, dissolved organic carbon.

Phytoplankton biomass dynamic

In March 2009, biomasses reached their highest value over the monitoring period (Fig. 3b). The biomass was mainly composed of microphytoplankton with a bloom of Dinoflagellates (*Peridinium gutwinskii* Woloszyńska and *Ceratium hirundinella* Bergh). Other biomass peaks of lesser magnitude were observed, ranging between 4x10^3 and 2.5x10^3 μg L^{-1} and mostly occurred during transition periods: i) at the end of the wet season, peaks were detected in November 2009 with some *Peridinium* spp. and in September 2011 with Chlorophyta-Dinoflagellates assemblages. By the end of the warm season and the beginning of the wet season, like in August 2010, high biomasses were maintained by some Dinoflagellates; ii) between warm and wet seasons, in May and June 2011, the high biomass was mainly composed by some small sized taxa - *e.g.*, *Crucigeniella* spp. Lemmermann, *Dictyosphaerium sphagnale* Hindák, *Oocystis parva*, *Tetrastrum komarekii* and *Tetraedron caudatum*. There was also a positive correlation between phytoplankton biomass and surface water temperature (Spearman r=0.36, $P<0.05$).

The lowest biomasses (<1x10^3 μg L^{-1}) were typically recorded at the peak of the wet season (between June and August 2009) and during the cool dry period (between January and February in 2010 and 2011).

Functional groups dynamic

Phytoplankton communities from NT2 Reservoir were composed by 22 functional groups. The main groups and their different genera are represented in the Tab. 3. The most abundant are Lo, F, A and P; they represented 57%, 10.5%, 4.5% and 4% respectively of the total biomass recorded during the study. The dynamics of the main functional groups are illustrated in Fig. 5 a-c. The functional groups Lo, Y and W2 were dominant at the beginning of the study and steadily decreased throughout the monitoring period. In 2009, the group Lo was strongly dominant contributing up to 82% of total biomass (Fig. 5a). Since April 2009, co-occurrence of two new groups appeared. It concerned Y significantly represented by *Cryptomonas reflexa* Skuja and W2 group (*Trachelomonas* spp. Ehrenberg). Between June and July, Y co-occurred with F gathering more than 62% of the total biomass. In October and November 2009, the Dinoflagellates, belonging to group Lo, obviously sustained the biomasses. In 2011, the group Lo declined to 8.4% of total biomass. The association (X1-J) co-dominated the assemblages with the groups (E-F) from the beginning of the 2010 cool dry season

(Fig. 5b). They sustained 85% of total biomass in February 2010. During stratification period, the (E-F) assemblages persisted whereas (X1-J) declined. At the end of the wet season, in October, the group A reached 27% of total biomass. We recorded the following sequence: (A-X1-J) à (F-N-P) (Fig. 5c). The associations (A-Lo-E-F-X1-J) dominated the biomasses by the end of 2010.

Although monthly biomasses were generally lower than the previous years, 2011 is marked by the occurrence of new associations groups. In early March, green algae growth was dominated by (E-F-J) assemblages alike in 2010. In June, at the top of stratification period, this association was followed by the group G for the first time. It supported 50% of the total biomass. Generally, during stratification, biomass was sustained by (N-P-F). During heaviest rains, especially in July and in August, the biomasses of all the groups significantly declined. By the end of wet season in October, only (E-F) maintained their growth in association with a relative growth of group G and Lo. In March 2011, at the beginning of the warm dry season, phytoplankton was mainly composed of A-Lo-E and F assemblages.

Structuring effect of environmental parameters on functional group and species abundances

Multi response permutation procedure

Results of MRPP carried out on phytoplankton communities expressed with functional groups and species abundances are shown on Fig. 6. The results show similar trends on functional groups and species assemblage's structure. For both, the year presents the strongest A-statistic scores ($P<0.05$). The highest score is obtained with functional groups. Dam outflows are also a significant determinant driver structuring the assemblages ($P<0.05$). Water level and Dam outflows have more important structuring impact ($P<0.05$) on species than on functional groups ($P>0.05$). Functional groups are significantly affected by pH ($P<0.05$), whereas species are much less impacted by this variable ($P>0.05$). On the other hand, species are signifi-

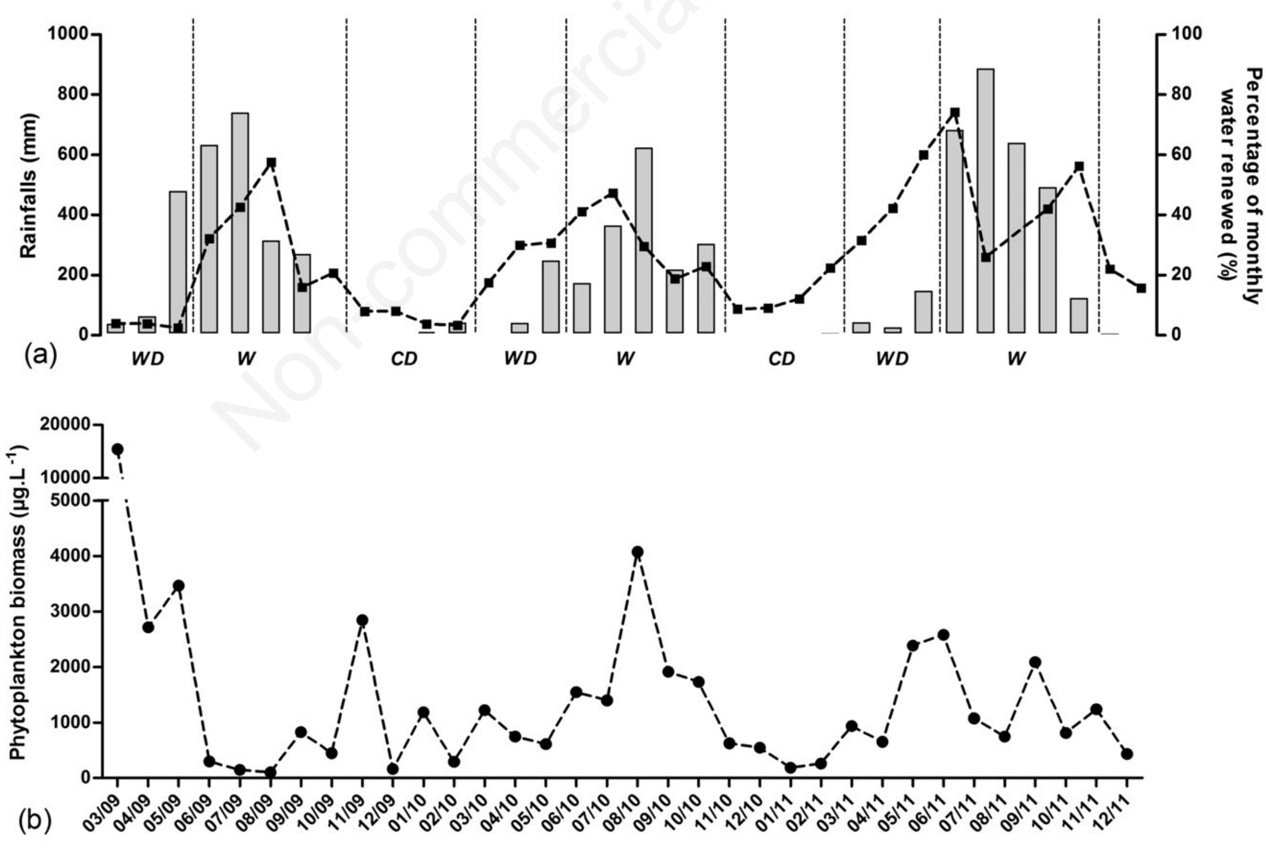

Fig. 3. a) Hydrological characteristics of the NT2 Reservoir following the percentage of monthly water renewed (black square) with rainfall (grey bar) and b) phytoplankton biomass evolution (black dot) from March 2009 to December 2011. CD, cool dry season; WD, warm dry season; W, wet season.

cantly impacted by seasons ($P<0.05$), whereas functional group are less impacted ($P>0.05$). DOC also explains phytoplankton communities variability (expressed with functional groups or species). A very significant and positive correlation between DOC concentrations and phytoplankton biomasses is observed (Spearman $r=0.49$, $P<0.0035$). Total phosphorous concentrations have no effect on functional groups and species structure. However, total nitrogen concentrations are significantly correlated with functional groups and species ($P<0.05$).

Indicator species analysis

Indicator value (IndVal) indices and calculations for phytoplankton species and for functional groups were computed for five parameters showing significant results with the MRPP test. The indicator species and functional groups were pooled in four categories according to their inter-annual dynamics (Tab. 4). They were categorized in accordance with the assemblage they belong to such as *pioneer*, *transitional*, *colonizing* and *permanent*. The functional groups and species presenting a decline of their biomass along the years belong to the *pioneer* assemblages; those showing a transitory effect were gathered into the *transitional*; those presenting an increase of their biomass along the year were gathered into the *colonizing* and those having a stable abundance were considered as *permanent*".

The indicator taxa belonging to the pioneer assemblages (*Peridinium willei* Lo and *Cryptomonas reflexa* Y) significantly indicated medium to high TN at the beginning to the study. Furthermore, they were good indicators of high pH. All of these species and functional groups are mixotrophic. The indicative species and functional groups of this pioneer assemblage were characterized by mixotrophic and motile traits (*e.g.*, *Cryptomonas reflexa, Peridinium* sp.). In the transitional groups, X1 and *Tetraedron caudatum*, were indicators of the year 2010. Group J had an affinity for high DOC during stratification period. The indicators taxa of the colonizing group, were functional groups G, N and also *Staurastrum* cf. *punctulatum* which are all heterotrophic taxa. Group N was indicator of very high TN, high pH values and DOC. Some colonial Chlorophyta which belong to group F are an indicator of environmental situations. As shown in Tab. 4, *Botryococcus braunii* Kützing is an indicator of high pH value, *Gloeocystis sp.* Nägeli indicates low DOC and *Elakatothrix gelatinosa* Wille indicates strong water decrease.

We can observe that some species are only indicators of hydrological parameters, *e.g.*, *E. gelatinosa*, *Staurastrum tetracerum* Ralfs ex Ralfs is an indicator for low outflows and *Staurastrum* cf. *punctulatum* Brébisson has shown a very significant indicative value for the increase of water level.

DISCUSSION

Interannual variability of phytoplankton communities: importance of colonization processes

The successions of the phytoplankton assemblages at NT2 Dam site, reflected a strong interannual variability and these annual changes in phytoplankton community were greater than those detected at the seasonal scale.

Diversity (Shannon index) confirms the high inter-an-

Tab. 2. Summary of physical and chemical data measured at the sub-surface in Nam Theun 2 Reservoir at the dam site location, with medians of annual values from 2009-2011 and stratification period (from March to September) (Median [Min-Max]).

	2009		2010		2011	
	Annual values	Stratification period	Annual values	Stratification period	Annual values	Stratification period
Water temperature (°C)	26.7 (19-27.9)	27.5 (25.4-27.9)	26.4 (20.8-29.6)	28.8 (22.6-29.6)	24.2 (19.5- 29.3)	27.8 (20.1-29.3)
pH	6.5 (5.8-7.1)	6.75 (5.9-7.1)	6.7 (5.8-6.9)	6.7 (6.4-6.9)	6.8 (5.8-7.7)	6.9 (5.9-7.7)
Dissolved O_2 (mg L^{-1})	4.1 (0.9-7.4)	5.15 (3.6-7.4)	6.2 (2.1-7.7)	7.1 (3.7-7.7)	6.4 (3.8-8.8)	7.4 (4.5-8.8)
TSS (mg L^{-1})	3.6 (1.4-8.9)	3.8 (1.4-8.9)	3.7 (1.2-9.0)	3.8 (1.2-9.0)	1.8 (0.7-4.5)	2.5 (0.7-4.5)
Secchi depth (m)	1.7 (1.2-2.5)	1.7 (1.3-2.5)	1.8 (1.2-2.2)	1.8 (1.3-1.9)	2.1 (1.5-2.6)	1.95 (1.25-2.4)
TP (μg L^{-1})	0 (0-270)	12 (0-270)	0*	0*	0* (0-80)	0 (0-30)
TN (μg L^{-1})	130 (0-570)	0 (0-230)	500 (0-1000)	730 (0-930)	780 (0-1550)	765 (360-930)

*TSS, total suspended solids; TP, total phosphorous; TN, total nitrogen. *Below detection limit.*

nual variability: the assemblages present at the beginning of the impoundment were less diverse, and then progressively increased in diversity. The nascent communities of the NT2 Reservoir appeared to be well adapted to stressful conditions (Reynolds, 1988) of this newly impounded reservoir, which include a decrease of light availability (resulting from high suspended particle concentrations following impoundment). These stressful conditions limited the development of photoautotroph organisms especially green algae. The Lo functional group (Padisak *et al.*, 2009) was dominant at the beginning of the study; it is considered as an S-strategy species (Stress-tolerant). Du-

Tab. 3. The main functional groups found in NT2 Reservoir with the representative genera in accordance with their periods of occurrence.

Group code	Genus included in the group	Period of occurrence
Lo	*Peridinium*	From cool season up to warm and dry season
Y	*Cryptomonas, Gymnodynium*	Cool dry season - Wet season
W2	*Trachelomonas*	Mainly in 2009
A	*Cyclotella, Rhizosolenia*	June in 2010 and Sept.- Dec. in 2010 and in 2011
X1	*Ankistrodesmus, Monoraphidium*	Dry season in 2010 and 2011
X2	*Kephyrion, Rhodomonas*	Cool dry season - Wet season
J	*Crucigenia, Crucigeniella, Tetraedron, Tetrastrum, Coelastrum, Scenedesmus*	Dry season: Feb.- Mar. in 2010 and Nov. 10 - Jan. 11
N	*Cosmarium, Staurodesmus, Staurastrum*	April 2010; July-Aug. 2010 and Sept. 2010 Jan. 2011; April-July 2011 and Oct. 2011
P	*Closterium, Fragilaria*	Sept. 2009; July-Aug. 2010 and June-Aug. 2011
G	*Eudorina, Gonium*	Warm dry season in 2011 (March-May)
E	*Dinobryon, Mallomonas*	Jan.-Feb. 2010; May-June 2010; Feb.- April 2011; Aug.- Sept. 2011 and Nov.- Dec. 2011
F	*Botryococcus, Dictyosphaerium, Kirchneriella, Oocystis, Sphaerocystis*	June-July 2009; Sept. 2009; Dec. 2009 - July 2010; Sept. 2010 - Dec.2011

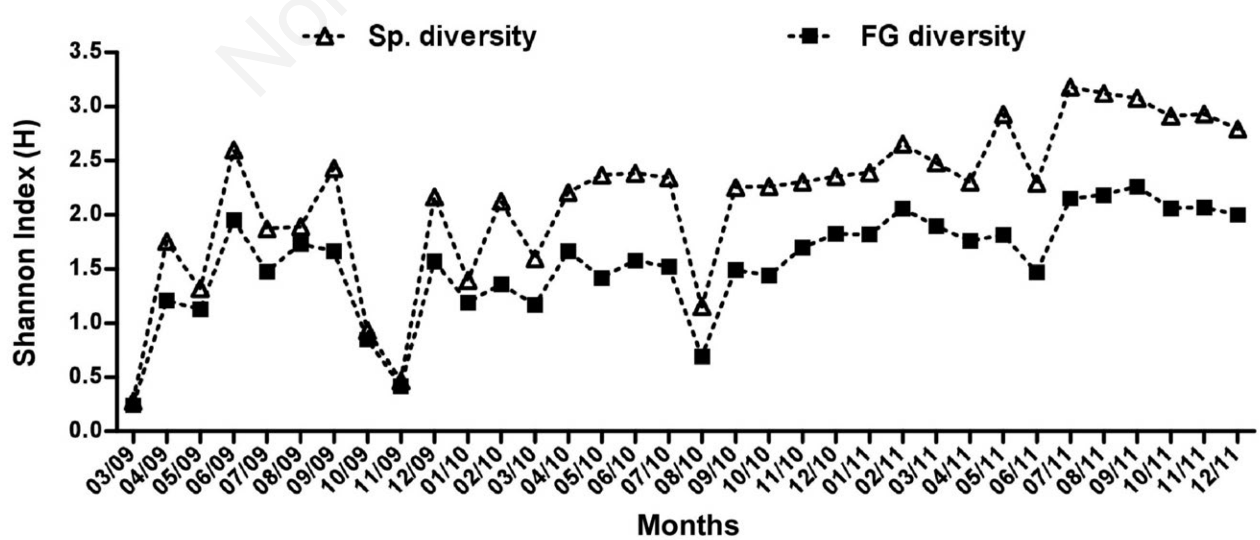

Fig. 4. Dynamic of the Shannon-Weaver diversity index (black dot) for species (black triangle) and functional groups (black square) from March 2009 to December 2011.

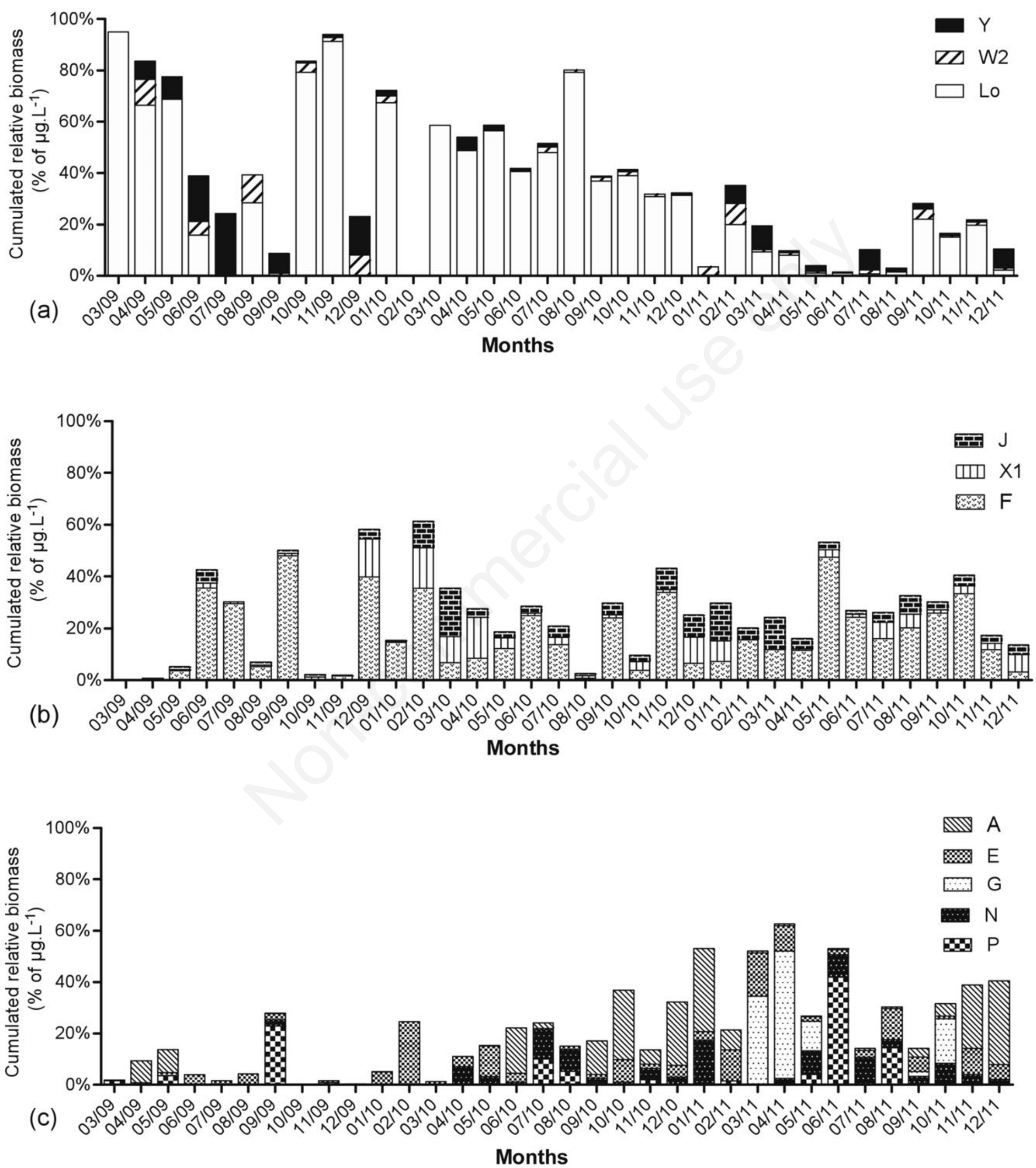

Fig. 5. Evolution of the cumulated relative biomasses expressed in percentage of total biomass (% of µg L^{-1}) for the different assemblages identified overt the study. a) Relative biomasses of some pioneers functional groups (Y, Lo and W2). b) Relative biomasses of some transitional functional groups (F, X1 and J). c) Relative biomasses of some functional groups (A E G N and P).

ring its impoundment, the NT2 Reservoir received a high amount of suspended particles. In early 2009, even if high water turbidity could limit plankton growth (Cherifi and Loudiki, 2002), the highest phytoplankton biomass was recorded at this time and was related to high organic matter (TSS concentrations and DOC). The Y functional group also had high biomass especially between June and July 2009, when there was a high percentage of water renewal. It is a fast growing, C-strategist algae (colonist, invasive; Reynolds 1980, 1984). These observations are in accordance with Brazilian studies where the functional group Y was known to prefer mixing period and a high turbidity because they had greater adaptability to water column mixing and low transparency conditions (Nabout *et al*., 2006). As suggested by Olrik (1994), the Lo-Y assemblage has a high probability of early colonization of new planktonic habitats. However the strong outflow and water renewal during the wet season in 2009 represent a cumulation of unfavorable conditions leading to the decline of group Lo, because this group is sensitive to prolonged or deep mixing (Reynolds *et al*., 2002; Huszar *et al*., 2003). Consequently, the efficiency of colonization of a young reservoir depends not only on environmental variables but also on the adaptive strategies of different types of algae, which at the end, constitute the ecological response of phytoplankton to environmental variability.

From 2010, the setting of an annual hydrological cycle involved a greater hydraulic stability during the warm dry season (low discharge and late rainfalls), and the increase of light availability. Such conditions favored the NT2 phytoplankton growth (Reynolds, 1998). The phytoplankton community became increasingly complex with new functional and taxonomic groups appearing along the study period. Cardinale (2011) showed that communities with higher biodiversity take advantage of the niche opportunities in an environment. The increase of functional and taxonomic diversity in NT2 Reservoir should therefore be a result of an increase in ecological niches complexity. Hydraulic stability is the major environmental descriptor which explains this niche diversification: the longer period of stratification measured since 2010 and the increase in water transparency offered conditions for a greater number of ecological niches.

Bottom-up factors structuring phytoplankton community in this newly impounded sub-tropical reservoir

Results demonstrate that hydrological balance is a relevant driver in NT2 phytoplankton community which explains its interannual dynamic. During the wet season in 2009 and in 2011, rainfalls and Dam spills might be the cause of turbulences disrupting water column stability. Such phenomenon has involved some changes in the phytoplankton community with a decrease in its biomasses. As shown by Harris and Baxter (1996), in reservoirs with seasonal thermal stratification patterns, inter annual changes in rainfalls could modulate the thermal structure of water column and override regular hydrological events.

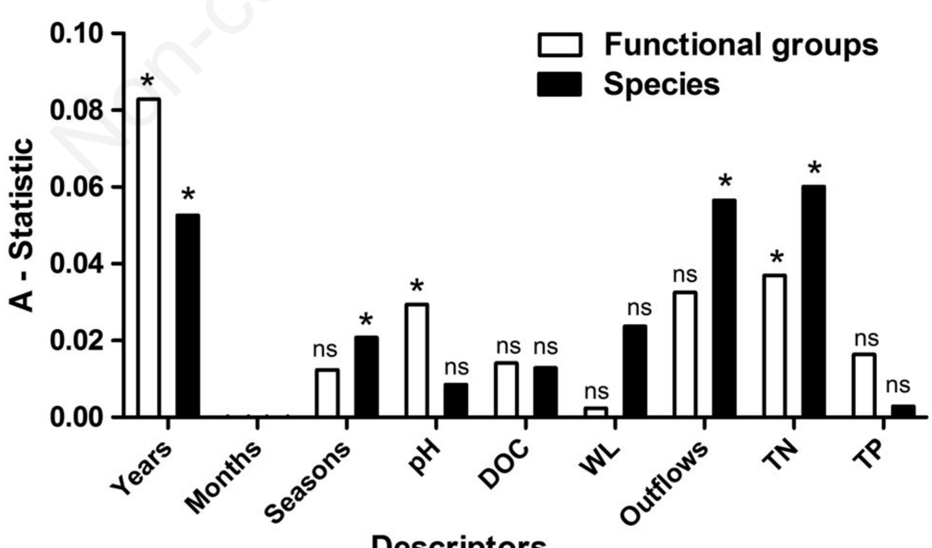

Fig. 6. Temporal and environmental parameters structuring the phytoplankton communities when expressed as species biomass or functional-groups biomasses. The A-statistic (calculated by an MRPP) provides an assessment of the communities heterogeneity for temporal descriptors as years, months, seasons, for chemical parameters as pH, total nitrogen (TN), total phosphorous (TP), dissolved organic carbon (DOC), and hydrological parameters as water level (WL), outflows from the dam (Outflows).

Subsequently, the hydraulic balance could create turbulences within the water column yielding irregular patterns of phytoplankton variability (Naselli Flores and Barone, 1998). Conversely, the thermal stratification period offers greater hydraulic stability with higher biomass and diversity. A previous study in Liuxihe Reservoir (China) has shown similar trends for tropical systems: two peaks of phytoplankton biomass occurred prior to and at the end of wet season (stratification periods; Xiao *et al*., 2011).

As seen in other reservoirs, hydrologic regimes may affect phytoplankton biomass and species composition by influencing nutrient dynamics in the water column (Costa *et al*., 2009). Several authors showed that species have particular preference for nutrients (*e.g*., Brettum, 1989; Wolfram and Dokulil, 2007). Although the nutrients concentrations are often mentioned as the key elements explaining phytoplankton variability, in the NT2 Reservoir phosphorous played no role in structuring the NT2 phytoplankton community compared to the colonization process. The W2 functional group was indicator of high nutrient concentrations: it is commonly found in mesotrophic ponds and shallow lakes (Reynolds *et al*., 2002).

How functional groups respond to bottom-up factors in NT2 Reservoir?

Reynolds' functional classification of freshwater phytoplankton (Reynolds *et al*., 2002) is probably the most frequently used non-taxonomic approach to group phytoplankton taxa. It has been successfully applied recently to investigate phytoplankton assemblages in South China reservoirs (Xiao *et al*., 2011; Hu and Xiao, 2012). Nevertheless, as demonstrated by Hu *et al*., (2013) functional groups can show a high degree of overlapping, but since coda are associated with very detailed environmental templates, this method was helpful in explaining phytoplankton variability in relation to environmental factors. The hydrological parameters (water renewal and outflow) were able to explain this variability. The changes in algal composition and biomass also occurred as a consequence of changes in the environmental conditions (temperature, light and nutrient concentrations) induced by the flush of surface water (Rigosi and Rueda, 2012). In our study, some functional groups were related to different structuring factors (hy-

Tab. 4. Indicator species and functional groups of the different parameters, calculated with the IndVal analysis. In the table, species and functional groups were sorted based on their interannual dynamic: pioneer (decrease of their relative abundance), transitional (increase and then decrease of their relative abundance), colonizing (increase) and permanent assemblages (stable relative abundance).

	Indication	IndVal	P value	Mixotrophy
Pioneer				
Lo	High pH	75.4	0.020	Yes
	Medium TN	72.5	0.009	
Peridinium willei	High TN	39	0.023	Yes
Cryptomonas reflexa	2009	61.8	0.003	Yes
Transitional				
X1	2010	50.1	0.005	No
J	High DOC	46.4	0.037	No
Tetraedron caudatum	2010	60.4	0.010	No
Colonising				
G (composed by *Eudorina elegans*)	2011	41.7 (33.3)	0.006 (0.027)	No
	Warm season	30.2 (31.3)	0.039 (0.011)	
X2 (composed by *Rhodomonas minuta*)	2011	58.9 (58.1)	0.014 (0.009)	Yes
N (composed by *Staurastrum tetracerum*)	Very high DOC	69.8 (62.1)	0.005 (0.006)	
	Very high TN	74.8 (58.1)	0.002 (0.006)	
	High pH	63.1	0.02	No
	(Low outflow)	(65.0)	(0.010)	
Staurastrum cf. punctulatum	Increase of level	60.0	0.003	No
Permanent				
(species belonging to group F)				
Botryococcus braunii	2011	58.3	0.001	No
	High pH	53.8	0.008	
Gloeocystis sp.	Low DOC	40.0	0.015	No
Elakatothrix gelatinosa	Sharp level decrease	44.1	0.025	No
Small Chlorophyceae	Low outflow	40.5	0.021	No
	Very high TN	28.7	0.009	

DOC, dissolved organic carbon; TN, total nitrogen.

drodynamism, DOC, nutrients and pH) and therefore can be of interest for biomonitoring purposes.

According to IndVal analyses, the small green algae were indicator of water level increase. On the other hand, *Elakatothrix gelatinosa*, a representative species of group F, indicated water level decrease over the stratification period. Colonial Chlorophytes from F group, including *Botryococcus*, are usually known to be tolerant to stratification, high insolation and low nitrogen and phosphorus concentrations (Goldman and Jassby, 2001). Although DOC varies greatly at the interannual scale, DOC variations were significantly correlated to phytoplankton biomass. High biomass of phytoplankton could coincide with relatively high DOC concentrations because algae can produce DOC (*e.g*., mucilage) and also because of cell lysis delivering DOC in water. This phenomenon was observed by Thurman (1985) who observed increase of DOC concomitant with high photosynthetic activities. In our study we can assume a direct link between DOC and phytoplankton. However, we cannot conclude if high DOC concentrations provoke or not an increase of the NT2 phytoplanktonic biomass. However, the DOC played a role in structuring the assemblages. In the NT2 Reservoir, during the stratification period a phytoplanktonic succession occurred following a gradient of DOC concentrations from 0 to 4 mg L^{-1}:

Gloeocystis sp. ('F') → 'X2' (*Rhodomonas minuta*) → 'J' → 'N' and *Staurastrum tetracerum*

Primary production is one of the major metabolic pathways by which organic matter is produced and destroyed (Cole *et al*., 2000). Moreover, because DOC can provide an important source of energy for microorganisms (Tranvik, 1992), DOC can be used as a marker of trophic level resources kinetic in aquatic ecosystem (Janson, 1998; Jones, 1998; Lampert and Sommer, 2007). This study shows that DOC can also be used as a proxy of phytoplankton biomass. Group A is usually considered as good indicators of trophic level thanks to their tolerance for nutrient depletion, especially phosphorus deficiency (Reynolds *et al*., 2002). This group, represented by *Cyclotella* and *Rhizosolenia*, is frequently associated with high light intensity during stratification (Sarmento *et al*., 2006; Xiao *et al*., 2011). The longest stratification period and lower water level may account for the group A in the NT2 Reservoir. However, the IndVal analyses showed that the warm season favoured the group G (*Eudorina elegans*) which belongs to a nutrient-rich habitat in stable water columns found in storage reservoir (Reynolds *et al*., 2002). According to the MRPP results, pH is determinant important in explaining community structure, especially functional groups (as opposed to species composition). The groups Lo and N occurred preferentially in pH values above 7 from the end of warm dry season and, with moderate disturbance, their occurrence is also reported during the wet season when water level increases. Highest pH values were observed likely due to photosynthetic activity of these groups. For instance, at the beginning of the investigations highest biomass referred to a high photosynthetic activity from the group Lo. Group N also indicated high TN, pH and DOC; this group is usually present in shallow lakes as well as in the epilimnia of stratified lakes (Padisák *et al*., 2009). Nevertheless, only one species is indicating particular pH values: *Botryococcus braunii* which has a significant affinity for high pH values. During such period, highest pH values and lowest transparency are indicative of a higher trophic status, even though a relative low nitrate and phosphate concentrations have been measured (Silva *et al*., 2005).

CONCLUSIONS

The NT2 Reservoir displayed a good example of phytoplanktonic successions during the colonization of a recently created habitat. The hydraulic balance was identified as the principal factors that controlled algae development and composition. Intense disturbances (rainfalls, strong discharge and high percentage of water renewed) reduced phytoplankton biomasses and diversity. The impoundment of the reservoir contributed to an increase of water turbidity favouring the dominance of the S-C- strategists (Lo-Y) with low diversity during the first months of this monitoring. The diversification of the phytoplankton community after impoundment is related to a greater hydraulic stability and a water transparency increase.

Our results also demonstrate that the functional groups A, F, X2, J and N are indicator of particular trophic level assessment and DOC concentrations. The NT2 Reservoir can be characterized as a meso-oligotrophic water body where phytoplankton community is principally controlled by the interannual variations of environmental variables and enables describing the following succession: X1-J-(Lo); Lo-(G); P-N; A-X1, which correspond to a transition from mesotrophic to meso-oligotrophic taxa. Our study demonstrates the applicability of functional groups for biomonitoring trophic level. They even better contributes to understand the interannual dynamic than taxonomy level. In the future, the understanding of the relationship between DOC and phyto biomass occurring in the NT2 Reservoir should be further investigated.

ACKNOWLEDGMENTS

This research has been conducted at the Aquatic Environment Laboratory of Nam Theun 2 Power Company in Laos whose Shareholders are Électricité de France, Lao Holding State Enterprise and Electricity Generating Public Company Limited of Thailand.

The authors would like to thank the Nam Theun 2 Power Company (NTPC) for providing the logistic support on site related to field activities. We are also grateful to the team of the Aquatic Environment Laboratory (AEL) for chemistry analyses and their help given during field trips. Finally, we are thankful to Mr. Paul Dumbrell and Ms Léah Bêche, who reviewed and improved this version of the manuscript as a native English-speaking.

REFERENCES

AFNOR, 2006. Water quality. Guidance standard on the enumeration of phytoplankton using inverted microscopy (Utermöhl technique). EN 15204. Afnor: 39 pp.

Anneville O, Souissi S, Ibanez F, Ginot V, Druart JC, Angeli N, 2002. Temporal mapping of phytoplankton assemblages in Lake Geneva: annual and interannual changes in their patterns of succession. Limnol. Oceanogr. 47:1355-1366.

APHA, 1995. Standard methods for examination of water and wastewater, 19th ed. American Public Health Association, Washington DC, USA.

Biondini ME, Bonham CD, Redente EF, 1985. Secondary successional patterns in a sage brush (Artemisia tridentata) community as they relate to soil disturbance and soil biological activity. Vegetation 60:25-36.

Boonsoong B, Sangpradub N, Barbour MT, Simachaya W, 2008. An implementation plan for using biological indicators to improve assessment of water quality in Thailand. Environ. Monit. Assess. 165:205-215.

Bourrelly P, 1981. [Les algues d'eau douce: les algues jaunes et brunes].[Book in French]. . Boubée et Cie: 438 pp.

Bourrelly P, 1985. [Les algues d'eau douce: les algues bleues et rouges].[Book in French]. Boubée et Cie: 512 pp.

Bourrelly P, 1990. [Les algues d'eau douce: les algues vertes].[Book in French]. Boubée et Cie: 572 pp.

Brettum P, 1989. [Algen als Indikatoren für die Gewässerqualität in norwegischen Binnenseen].[Book in German]. NIVA: 102 pp.

Buzzi F, Dalmiglio A, Garibaldi L, Legnani E, Marchetto A, Morabito G, Salmaso N, Tartari G, Thaler B, 2007. [Indici fitoplanctonici per la valutazione della qualità ecologica dei laghi della regione alpina].[Document in Italian]. Ministero dell'Ambiente e della Tutela del Territorio e del Mare.

Calijuri MC, Dos Santos ACA, 2001. Temporal variations in phytoplankton primary production in a tropical reservoir (Barra Bonita, SP - Brazil). Hydrobiologia 445:11-26.

Cardinale BJ, 2011. Biodiversity improves water quality through niche partitioning. Nature 472:86-89.

Chanudet V, Fabre V, Van Der Kaaij T, 2012. Application of a three-dimensional hydrodynamic model to the Nam Theun 2 Reservoir (Lao PDR). J. Great Lakes Res. 38:260-269.

Cherifi O, Loudiki M, 2002. [Variations de la structure trophique du lac-réservoir oligotrophe Bin El Ouidane (Maroc)].[Article in French]. Rev. Sci. Eau 15:193-208.

Cole JJ, Pace ML, Carpenter SR, Kitchell JF, 2000. Persistence of net heterotrophy in lakes during nutrient addition and food web manipulations. Limnol. Oceanogr. 45:1718-1730.

Costa L, Huszar VLM, Ovalle A, 2009. Phytoplankton functional groups in a tropical estuary: hydrological control and nutrient limitation. Estuar. Coasts 32:508-21.

Coley PD, Bryant JP, Chapin FS, 1985. Resource availability and plant antiherbivore defense. Science 230:895-899.

Cowles HC, 1899. Ecological relation of the vegetation on sand dunes of Lake Michigan. Bot. Gaz. 27:95-117.

Crossetti LO, Bicudo CEM, 2005. Structural and functional phytoplankton responses to nutrient impoverishment in mesocosms placed in a shallow eutrophic reservoir (Garças Pond), São Paulo, Brazil. Hydrobiologia 541:71-85.

Descy JP, Tarbe AL, Stenuite S, Pirlot S, Stimart J, Vanderheyden J, Leporcq B, Stoyneva MP, Kimirei I, Sinyinza D, Plisnier PD, 2010. Drivers of phytoplankton diversity in Lake Tanganyika. Hydrobiologia 653:29-44.

Dillon PJ, Rigler FH, 1974. The phosphorus-chlorophyll relationships in lakes. Limnol. Oceanogr. 19:767-773.

Dufrêne M, Legendre P, 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol. Monogr. 67:345-366.

EDF-DTG, 2012. Report: Nakai Reservoir on the Nam Theun River, capacity curve calculation, 2012 data. Grenoble: 9 pp.

Finlay BJ, Esteban GF, 2001. Exploring Leeuwenhoek's legacy: the abundance and diversity of protozoa. Int. Microbiol. 4:125-133.

Grime JP, 1979. Plant strategies and vegetation processes. 4. J. Wiley & Sons, New York: 254 pp.

Goldman CR, Jassby AD, 2001. Primary productivity, phytoplankton and nutrient status in Lake Baikal, p. 111-125. In: M. Munawar and R.E. Hecky (eds.), Exploring the great lakes of the world: food-web, health and integrity. Backhuys Publishers.

Happey-Wood VM, 1988. Ecology of freshwater planktonic green algae, p. 175-226. In: C.D. Sandgreen (ed.), Growth and reproductive strategies of freshwater phytoplankton. Cambridge University Press.

Harris GP, Baxter G, 1996. Interannual variability in phytoplankton biomass and species composition in a subtropical reservoir. Freshwater Biol. 35:545-560.

Hindák F, 1984. Studies on chlorococcal algae (Chlorophyceae) III. Biologicke Práce: 320 pp.

Hindák F, 1988. Studies on chlorococcal algae (Chlorophyceae) IV. Biologicke Práce: 264 pp.

Hindák F, 1990. Studies on chlorococcal algae (Chlorophyceae) V. Biologicke Práce: 226 pp.

Hu R, Xiao LJ, 2012. Functional classification of phytoplankton assemblages in reservoir of Guangdong Province, South China. In: B-P. Han and Z. Lui (eds.), Tropical and Subtropical reservoir limnology in China. Monogr. Biol. 91:59-70.

Hu R, Han B, Naselli-Flores L, 2013. Comparing biological classifications of freshwater phytoplankton: a case study from South China. Hydrobiologia 701:219-233.

Huszar V, Kruk C, Caraco N, 2003. Steady-state assemblages of phytoplankton in four temperate lakes (NE USA). Hydrobiologia 502:97-109.

Janson M, 1998. Nutrient limitation and Bacteria - Phytoplancton interactions in humic lakes. In: D.O. Hessen and L.J. Tranvik (eds.), Aquatic humic substances. Ecol. Stud. 133:177-195.

Jeppesen E, SØndergaard M, Mazzeo N, Meerhoff M, Branco CC, Huszar V, Scasso F, 1999. Lake restoration and biomanipulation in temperate lakes: relevance for subtropical and tropical lakes, p. 341-359. In: M.V. Reddy (ed.), Tro-

pical Eutrophic lakes: their restoration and management. CRC Press.
Jones RI, 1998. Phytoplankton, primary production and nutrient cycling. In: D.O. Hessen and L.J. Tranvik (eds.), Aquatic humic substances. Ecol. Stud. 133:145-175.
Jung SW, Nguyen VV, Nguyen QH, Bae YJ, 2008. Aquatic insect faunas and communities of a mountain stream in Sapa Highland, northern Vietnam. Limnology 9:219-229.
Kaiblinger C, Anneville O, Tadonleke R, Rimet F, Druart JC, Guillard J, Dokulil MT, 2009. Central European water quality indices applied to long-term data from peri-alpine lakes: test and possible improvements. Hydrobiologia 633:67-74.
Krienits L, Kasprazak P, Koschel R, 1996. Long-term study on the influence of eutrophication, restoration and biomanipulation on the structure and development of phytoplankton communities in Feldberger Haussee (Baltic Lake District, Germany). Hydrobiologia 330:89-110.
Kruk C, Huszar VLM, Peeters ETH, Bonilla S, Costa L, Lürling M, Reynolds CS, Scheffer M, 2010. A morphological classification capturing functional variation in phytoplankton. Freshwater Biol. 55:614-627.
Lampert W, Sommer U, 2007. Limnoecology: the ecology of lakes and streams, 2. Oxford University Press: 324 pp.
Lund JWG, 1965. The ecology of the freshwater phytoplankton. Biol. Rev. 40:231-293.
Mastin BJ, Rodgers JH Jr, Deardorff TL, 2002. Risk evaluation of cyanobacteria-dominated algal blooms in a North Louisiana reservoir. J. Aquat. Ecosyst. Stress Recov. 9:103-114.
McCune B, Mefford J, 2006. PC-ORD. Multivariate Analysis of Ecological Data, ver. 5.18. MjM Software, Gleneden Beach.
Mieleitner J, Borsuk M, Burgi HR, Reichert P, 2008. Identifying functional groups of phytoplankton using data from three lakes of different trophic state. Aquat. Sci. 70:30-46.
Nabout JC, Nogueira IS, Oliveira LG, 2006. Phytoplankton community of floodplain lakes of the Araguaia River, Brazil, in the rainy and dry seasons. J. Plankton Res. 28:181-193.
Naselli Flores L, Barone R, 1998. Phytoplankton dynamics in two reservoirs with different trophic state (Lake Rosamarina and Lake Arancio, Sicily, Italy). Hydrobiologia 369-370:163-178.
Olrik K, 1994. Phytoplankton ecology: determining factors for the distribution of phytoplankton in freshwater and the sea. Danish Ministry of Environment: 183 pp.
Padisák J, Crossetti LO, Naselli-Flores L, 2009. Use and misuse in the application of the phytoplankton functional classification: a critical review with updates. Hydrobiologia 621:1-19.
Poikane S, 2009. Water Framework Directive intercalibration technical report. Part 2: Lakes. EUR 28838 EN/2, Office for Official Publications of the European Communities, Luxembourg.
Prygiel J, Haury J, 2006. Monitoring methods based on algae and macrophytes, p. 155-170. In: G. Ziglio, M. Siligardi and G. Flaim G (eds.), Biological monitoring of rivers: applications and perspectives. J. Wiley & Sons.
Reynolds CS, 1980. Phytoplankton assemblages and their periodicity in stratifying lake systems. Holartic Ecol. 3:141-159.
Reynolds CS, 1984. Phytoplankton periodicity: the interactions of form, function and environmental variability. Freshwater Biol. 14:11-142.
Reynolds CS, 1988. Functional morphology and the adaptative strategies of freshwater phytoplankton, p. 388-433. In: C.D. Sandgren (ed.), Growth and reproductive strategies of freshwater phytoplankton. Cambridge University Press.
Reynolds CS, 1998. What factors influence the species composition of phytoplankton in lakes of different trophic status. Hydrobiologia 369-370:11-26.
Reynolds CS, Huszar V, Kruk C, Naselli-Flores L, Melo S, 2002. Towards a functional classification of the freshwater phytoplankton. J. Plankton Res. 24:417-428.
Richard S, Arnoux A, Cerdan P, 1997. [Evolution de la qualité physico-chimique des eaux de la retenue et du tronçon aval depuis le début de la mise en eau du barrage de Petit-Saut].[Article in French]. Hydroecol. Appl. 1-2:57-83.
Rigosi A, Rueda FJ, 2012. Hydraulic control of short-term successional changes in the phytoplankton assemblage in stratified reservoirs. Ecol. Eng. 44:216-226.
Sabater S, Artigas J, Durán C, Pardos M, Romaní AM, Tornés E, 2008. Longitudinal development of chlorophyll and phytoplankton assemblages in a regulated large river (the Ebro River). Sci. Total Environ. 404:196-206.
Sarmento H, Isumbisho M, Descy JP, 2006. Phytoplankton ecology of Lake Kivu (Eastern Africa). J. Plankton Res. 28:815-829.
Schagerl M, Oduor SO, 2008. Phytoplankton community relationship to environmental variables in the three Kenyan Rift Valley saline-alkaline lakes. Mar. Freshwater Res. 59:125-136.
Schindler DW, 1978. Factors regulating phytoplankton production and standing crop in the world's freshwaters. Limnol. Oceanogr. 23:478-486.
Silva CA, Train S, Rodrigues LC, 2005. Phytoplankton assemblages in a Brazilian subtropical cascading reservoir system. Hydrobiologia 537:99-109.
Shannon CE, Weaver W, 1949. The mathematical theory of communication. University of Illinois Press: 144 pp.
Starmach K, 1972. [Chlorophyta III]. In: K. Starmach (ed.) [Flora Słodkowodna Polski]. [Book in Polish]. Polska Akademia Nauk, Instytut botaniki.
Starmach K, 1974. [Cryptophycea Dinophycea Raphidophycea]. In: K. Starmach (ed.) [Flora Słodkowodna Polski]. [Book in Polish]. Polska Akademia Nauk, Instytut botaniki.
Starmach K, 1983. [Euglenophyta]. In: K. Starmach (ed.) [Flora Słodkowodna Polski]. [Book in Polish]. Polska Akademia Nauk, Instytut botaniki.
Talling JF, 2001. Environmental controls on the functioning of shallow tropical lakes. Hydrobiologia 458:1-8.
Thornthon KW, Kimmel BL, Payne FE, 1990. Reservoir limnology: ecological perspectives. Wiley: 246 pp.
Thurman EM, 1985. Academic organic geochemistry of natural waters. Martinus Nijhoff/Dr.W. Junk: 68 pp.
Tilzer MM, 1990. Specific properties of large lakes, p 39-43. In: M.M. Tilzer and C. Serruya (eds.), Large lakes: ecological structure and function. Springer.
Tranvik LJ, 1992. Allochthonous dissolved organic matter as an energy source for pelagic bacteria and the concept of the microbial loop. Hydrobiologia 229:107-114.
Tundisi JG, Matsumura-Tundisi T, Abe DS, 2008. The ecological dynamics of Barra Bonita (Tietê River, SP, Brazil) reservoir: implications for its biodiversity. Braz. J. Biol. 68:1079-1098.
Utermöhl H, 1958. [Zur Vervolkomnung der quantitativen Phy-

toplankton: Methodik].[Article in German]. Int. Ver. Theor. Angew. 9:1-38.

Vollenweider RA, 1969. A manual on methods for measuring primary production in aquatic environments, 12. Blackwell Scientific: 213 pp.

Vollenweider RA, Kerekes JJ, 1980. Background and summary results of the OECD cooperative programme on eutrophication. OECD Publ.: 290 pp

Wetzel RG, Likens GE, 2000. Limnological analyses, 3. Springer: 429 pp.

Wolfram G, Dokulil MT, 2007. [Leitfaden zur Erhebung der biologischen Qualitätselemente. Teil B2, Phytoplankton]. [Book in German]. Lebensministerium Austria: 50 pp.

Wolfram G, Argillier C, De Bortoli J, Buzzi F, Dalmiglio A, Dokulil MT, Hoehn E, Marchetto A, Martinez PJ, Morabito G, Reichmann M, Remec-Rekar S, Riedmuller U, Rioury C, Schaumburg J, Schulz L, Urbanic G, 2009. Reference conditions and WFD compliant class boundaries for phytoplankton biomass and chlorophyll-a in Alpine lakes. Hydrobiologia 633:45-58.

Xiao LJ, Wang T, Hu R, Han BP, Wang S, Qian X, Padisák J, 2011. Succession of phytoplankton functional groups regulated by monsoonal hydrology in a large canyon-shaped reservoir. Water Res. 45:5099-5109.