Limnological Characterization and Flow Patterns of a Three-coupled Reservoir System and Their Influence on *Dreissena polymorpha* Populations and Settlement During the Stratification Period

Enrique Navarro[1,2]*, Montse Bacardit[1,2], Luciano Caputo[1,2], Toni Palau[3] and Joan Armengol[1,2]

[1]Dept. of Ecology, University of Barcelona
Av. Diagonal 645
08028 Barcelona, Spain

[2]GREAC, Barcelona Science Park
Florensa Building, Adolf Florensa s/n
08028 Barcelona, Spain

[3]Endesa (Enher-Fecsa)
Ctra. de Tarragona Km 89.3, Poligon Els Magraners
25008 Lleida, Spain

Abstract

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During summer 2001, zebra mussels (*Dreissena polymorpha* Pallas) were found (500 adults m^{-2}) in the coupled reservoir system composed by Mequinenza, Riba-Roja and Flix (Ebro River, Northeast Spain). Two years later, mussels achieved densities of 4000 adults m^{-2}, representing the first record of successful colonization by zebra mussels in the Iberian Peninsula. An August 2003 study investigated the environmental conditions that support the successful settlement of the zebra mussel populations during the stratification period. Flow patterns in the whole system and mussel populations near the dam were characterized. Chemical characteristics of water inputs, not the usual thermal stratification, determine the deep circulation of the Ebro River along the Riba-Roja reservoir, whereas water input from one tributary into Riba-Roja flows along the top of the water. Physico-chemical stratification of the water column seems to control the observed vertical distribution of zebra mussel biomass. Larger biomass and mean body size were found in the epilimnion, while meta- and hypolimnetic individuals were smaller in size and composed a lower biomass. Moreover, to know the influence of the water drawn off for electricity production in the settlement of mussel larvae, an artificial substratum (a rope) was placed in the influence area of the dam. Results indicate that flow conditions prevailing in the drawn-water layer may increase the attachment success of mussel larvae. Results show that during the stratification period the epilimnion of Riba-Roja was functioning as a "biological reactor" where *Dreissena* populations thrived.

Key Words: *Dreissena polymorpha*, zebra mussel settlement, reservoirs, thermal stratification, flow conditions, oxygen

* Corresponding author: EAWAG, Überlandstrasse 133, PO Box 611, 8600 Dübendorf, Switzerland, p: +41 44 8235134, f: +41 44 8235547, e-mail: enrique.navarro@eawag.ch

The zebra mussel (*Dreissena polymorpha* Pallas 1771) is a native species of the Black and Caspian seas region (Kinzelbach 1992). From the 19th century it began a rapid spread across European and North American water bodies, possibly initiated by human activities (Hebert *et al.* 1989). The high degree of connectivity between Eurasian and European water systems and ship trade between continents has facilitated the transport of colonizing animals across greater distances.

Zebra mussels have strong impacts on aquatic communities, affecting bacterioplankton (Cotner *et al.* 1995), fish, and other invertebrate assemblages (French III and Bur 1996, MacIsaac 1996). Infrastructures that depend on raw water (*i.e.*, electric power generation stations, drinking water treatment plants, industrial facilities and dam structures) have also been significantly impacted by zebra mussels. Thus, an increasing number of reports have focused on the physico-chemical conditions affecting zebra mussel physiology. However, few have approached the relationship between flow conditions and zebra mussel colonization success. Reservoir management practices could generate flow condition changes that could alter both the feeding and colonization behavior of mollusks (Eyster and Pechenik 1987, Archambault *et al.* 1999, Wacker and von Elert 2003). A study of the relationship between flow dynamics and mussel settlement and distribution of the populations could help predict their spread or colonization success and allow more effective prevention measures.

Zebra mussels were first seen in the Iberian Peninsula at the end of the 19th century when dead specimens were also found in the Duero River near Porto, in Portugal (Azpeitia Moros 1933). No other evidence of its presence was reported until 1982, when living young individuals were identified in the Llobregat River (northwest Spain). This population soon disappeared, however, washed out to sea by flash floods (Altaba 1992). Thus, establishment of this species in the Iberian peninsula is very recent, with first records registered in the lower reaches and reservoirs of the Ebro River (Altaba *et al.* 2001a, Altaba *et al.* 2001b).

Densities reached 500 ind m^{-2} in summer 2001 in the Ebro reservoir Riba-Roja (Altaba *et al.* 2001a, Altaba *et al.* 2001b). The overland movement of recreational boats is widely believed to be the primary vector for zebra mussel dispersal into inland water bodies (Carlton 1993, Johnson and Carlton 1996). For example, visiting fishermen from central Europe and other zebra mussel infested areas bring their boats to Spain, spreading zebra mussels (Altaba *et al.* 2001b).

Knowledge of the water flow dynamics for the three reservoirs and limnological variables possibly involved in the colonization success of the species during summer stratification, will be critical for investigating the potential environmental conditions supporting zebra mussel growth in the study reservoirs.
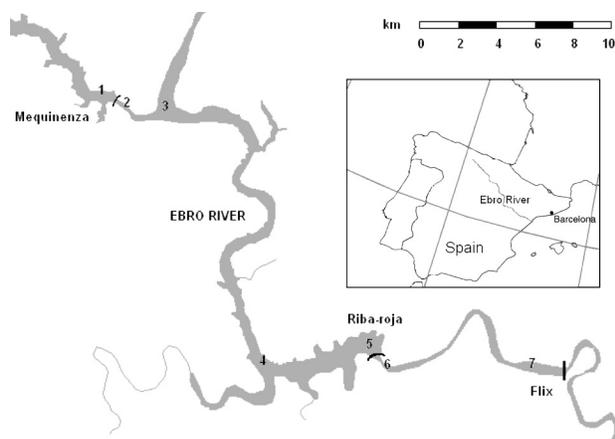

Figure 1.-Map showing sampling site locations along the river Ebro (northeast Spain). Station 3 was located at the entrance of the tributary River Segre to the Riba-Roja reservoir. Black lines between station1 and 2, between station 5 and 6 and downstream of station 7 are the dams of the three reservoirs in the study (upstream to downstream: Mequinenza, Riba-Roja and Flix).

Our hypothesis was that water stratification could play a major role in determining the distribution and establishment of the zebra mussel. Water flow dynamics could produce optimal epilimnetic environmental factors (high nutrient concentration, pH and dissolved oxygen) in comparison to those prevailing in the hypolimnion (McKillop and Harrison 1972, Sprung 1987, Hincks and Mackie 1997, Karatayev *et al.* 1998, Gelda *et al.* 2001). Moreover, the conditions prevailing in the drawn-water layer due to the water drawn off for electricity production may increase the attachment success of mussel larvae (Eyster and Pechenik 1987 Wacker and von Elert 2003).

Materials and Methods

Seven sites were sampled between August 4-6, 2003, across three coupled reservoirs in the Ebro River (northeast Spain). Mequinenza, the biggest (1533.79 hm^3 volume and 72.5 days residence time), is oligotrophic (TSI); Flix, also oligotrophic, is the smallest (11 hm^3 and 0.29 days); while the meso-trophic Riba-Roja is middle-sized (209.56 hm^3 and 11 days). Values were calculated using the flow data of the 30 days previous to the study.

Mequinenza, the most upstream of the three coupled reservoirs, was free of zebra mussels until 2004. At the time of the study, zebra mussels were present in Asco (unpublished data) 28 km downstream from Riba-Roja and Flix, where zebra mussel reported the highest densities (Altaba *et al.* 2001b) and appeared to be where zebra mussels were first introduced. Riba-Roja at the time of this study was the upstream spread limit of zebra mussel.
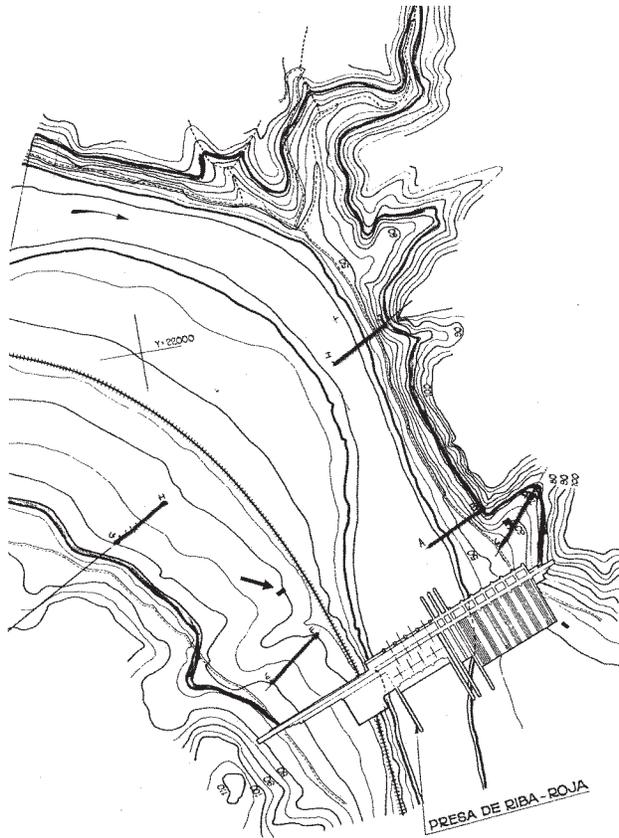
Figure 2.-Map showing the location of the 5 transects in the Riba-Roja reservoir used during the estimation of vertical distribution of zebra mussels in the reservoir basin. See methods for further details. Transects are shown as black solid lines. The black square, signaled by an arrow, was the location of the floating platform with a rope, for the study of zebra mussel colonization patterns.

Temperature, conductivity, oxygen, light, phosphorous and nitrogen profiles, chlorophyll *a* and zebra mussel veliger larvae sampling were conducted at sampling points 1, 5 and 7 (at the dam of each of the three reservoirs). At the rest of the sampling sites only physical profiles and veliger larvae samples were collected.

Temperature (°C), conductivity (μS cm^{-1}), dissolved oxygen (% saturation and mg l^{-1}) and pH were measured every 1 m down the water column to the bottom (Turo Water Quality Analyser model T-611 multiprobe). Conductivity was used as a tracer to determine the origin of the different water masses (layers). Total volumes were calculated for epilimnion (0-8 m), metalimnion (8-11 m), and hypolimnion (11-22 m) using the changes in conductivity and depths and used to estimate retention times for each layer (Armengol *et al.* 1999).

Light extinction coefficient was calculated using the underwater light profiles, performed using a Li-Cor LI-193 SA light sensor. Secchi depths were also measured.

Integrated water samples from the top 5 m and three samples from the hypolimnion (0-5, 18, 25 and 30 m in Mequinenza; 0-5, 8, 10 and 19 m in Riba-Roja) were taken. In the shallowest reservoir, Flix, samples from 0, 1, 2 and 6 m were taken. Hypolimnetic samples were taken with a 5-L UWITEC sampler. Chemical analyses were conducted on the samples to estimate suspended solids, total reactive phosphorus (TP), total nitrogen (TN; Grasshoff *et al.* 1983), soluble reactive phosphorus (SRP; Murphy, 1962) and alkalinity (Gran's method; Mackereth *et al.* 1978). In addition, the trophic state of each waterbody was described using the Trophic State Index (Carlson 1977).

Integrated samples for chlorophyll *a* were collected with a 5-m long tube sampler; concentration was estimated by filtration of a known volume onto GF/F filters following the trichromatic method (Jeffrey and Humphrey 1975). Integrated mussel larvae samples were collected using a 53-μm mesh Apstein net in 20-m vertical hauls at each sampling station. When depth was <20 m, we collected the zooplankton haul from bottom to surface. Samples were preserved in 4% formaldehyde (final concentration). Each subsample was allowed to settle in a sedimentation chamber and quantified with an inverted microscope (McCauley 1984).

A floating platform consisting of one 20-m long hemp rope was installed in Riba-Roja (Fig. 2) to identify any preferential vertical attachment distribution of zebra mussels in the water column. Zebra mussel density and biomass distribution (fresh drained weight) on the rope was measured at 1-m intervals, averaging the wet weight of all individuals attached on each meter. Five 100-m transects were selected in Riba-Roja running from shore to centre of the reservoir. Zebra mussel specimens were collected by divers at each sampling point with net bags (Fig. 2). Transects were selected to include various substrate types to sample a wide range of conditions available to the mussels down to a maximum depth of 30 m.

Linear regression was performed using Statistica 6.0 (Stat-Soft, Inc., Tulsa, USA). Sigma-restricted parameterization, confidence limits of 0.95 and significance level of 0.05 were applied.

Results

Water Circulation and Stratification

The main features of the water flow dynamics of the studied reservoirs were established using vertical measurements of temperature, conductivity and dissolved oxygen. The Ebro River flows rapidly through the hypolimnion of Riba-Roja (see retention times in Table 1), without experiencing sub-

Table 1.- Values of retention times, water extinction coefficient (K), chlorophyll *a* concentration in the 0-5 m surface layer, water transparency as Secchi depth (SD), suspended solids concentration (SS), ash free dry weight (AFDW) and averaged alkalinity (ppm bicarbonate) in the water column at the seven sampling sites (see Map for details).

Reservoirs	Mequinenza	Riba-roja				Flix	
Residence time (days)	72.5	5.28				0.29	
Sampling stations	1	2	3	4	5	6	7
K	0.356	0.626	2.426	0.694	0.600	0.693	0.437
Chl *a* (μg l^{-1})	3.18	-	-	6.81	8.95	1.82	1.98
SD (m)	2.5	2.1	0.52	2.15	2.95	2.45	4.96
SS (mg l^{-1})	5.619	-	-	2.600	4.780	3.375	3.375
AFDW (mg l^{-1})	2.286	-	-	1.000	2.341	1.750	1.625
Alkalinity (mg l^{-1})	170.5	-	-	-	163.4	-	184.6

stantial chemical changes in the water (Fig. 3). Water flow in Flix are similar to those of a stream (see retention times in Table 1). During summer, warm water from the Segre River, a tributary of the Ebro River, flow directly into the epilimnion of the Riba-Roja reservoir. Thus, the Segre water, having a relatively low density, flows above the cold, heavier water draining from Mequinenza. At station 4, strong stratification of the water column established during the summer, not due to the typical differential warming of the water column, but rather to the input of two water masses of distinct densities. Downstream of station 4, the thermocline could be seen to erode as a result of water drawn off for electricity production at Riba-Roja hydropower plant (see station 5 in Fig. 3). An intermediate layer was formed due to the mixing of top and bottom layers, with intermediate chemical characteristics. At the time of this study (August), this layer was of relatively small volume (*i.e.*, epilimnion 0-8 m depth, 111.16 hm³; metalimnion 8-11 m, 29.64 hm³; hypolimnion 11-bottom, 58.77 hm³). Retention times of the three layers were 85.04, 5.78 and 12.23 days, respectively. Flix functioned truly as a river, carrying the cold water draining from the hypolimnion of Riba-Roja downstream.

Mean pH was 8.16 at the surface and 7.72 at 8 m deep in Riba-Roja and Mequinenza reservoirs. Below 8 m, mean deep pH was about 7.70. The Ebro water showed a higher conductivity than that of the Segre River, flowing near the bottom at stations 3, 4 and 5 (Fig. 3). Dissolved oxygen profiles were consistent with those of temperature and conductivity. In summary, the chemical characteristics of water inputs determine the deep circulation of the Ebro River along the system of reservoirs, whereas the Segre water input into Riba-Roja flows along the top of the water column.
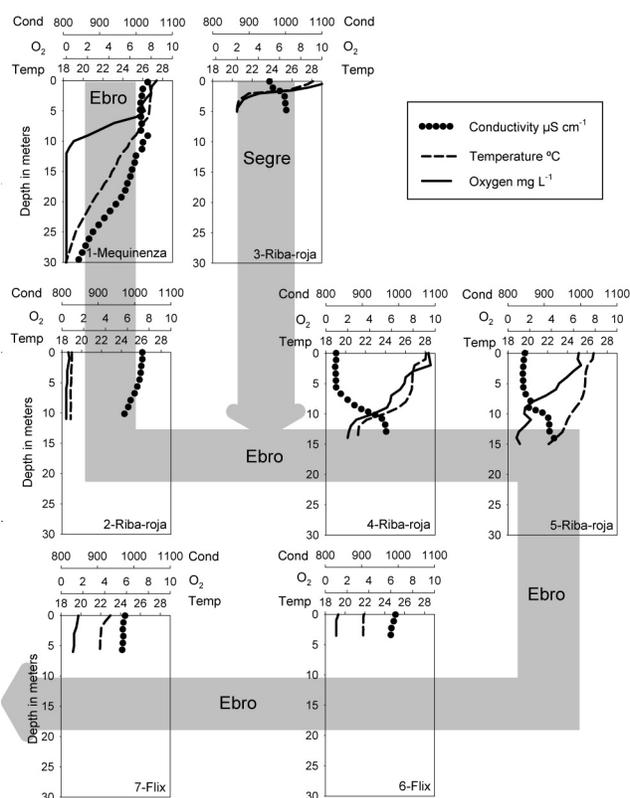

Figure 3.- Vertical profiles of temperature, conductivity and oxygen concentration at the 7 sampling stations from upstream to downstream (follow grey arrow). Despite the strong influence of biological processes on dissolved oxygen concentrations in the water, the sequence of oxygen vertical profiles along the three reservoirs (upstream to downstream: Mequinenza, Riba-Roja and Flix) suggests the deep circulation of oxygen-poor Ebro waters.
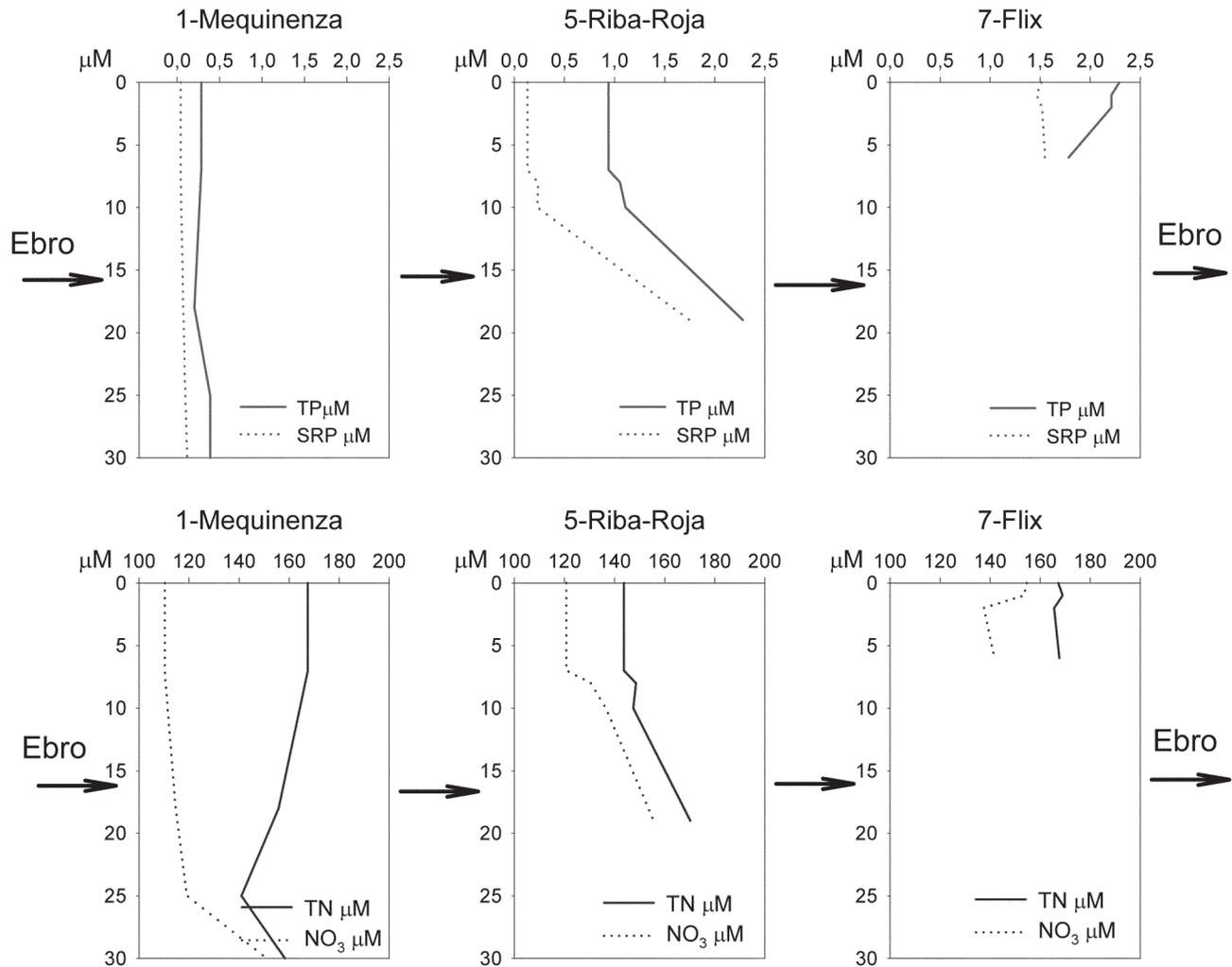
Figure 4.-Vertical profiles of phosphorus (upper panels) and nitrogen (lower panels) concentrations at the three study reservoirs (Mequinenza, Riba-Roja and Flix). The direction of water flow is shown by the arrows between panels.

Chlorophyll **a** *and Water Transparency*

Chlorophyll *a* concentration increased from Mequinenza to Riba-Roja dam, whereas it was substantially reduced in the Flix reservoir. Water transparency increased after traveling through the reservoirs of Riba-Roja and Flix (Table 1). The Segre water had the lowest Secchi disk depth and the highest extinction coefficient of the sampling stations, likely due to its high content of suspended matter (see suspended solids in Table 1). Stations near the dam of Flix reservoir showed the highest transparency of sampling sites in this study. Light reached the bottom of riverine zones in the Riba-Roja and Flix reservoirs, allowing the growth of macrophytes (stations 2, 6 and 7).

Nutrients and Alkalinity

Nutrient concentrations in the hypolimnion were often higher than in the epilimnion. Nutrient profiles showed little vertical and longitudinal variability across reservoirs (Fig. 4). Nitrate concentrations ranged from 110 to 155 µM (140-170 as total nitrogen). Because N:P ratios were higher than 16 (Fig. 5), and SRP concentration was below 10^{-7} M, primary production was probably limited by phosphorus availability in the water. Carbonate alkalinity in the three reservoirs was between 170 and 184 mg l^{-1}.

Dreissena *Larvae and Adults*

No *Dreissena* larvae were in Mequinenza (station 1) or at sampling stations 2 and 3 in Riba-Roja. Veligers were present only downstream of sampling station 4 (32 ind l^{-1}), with
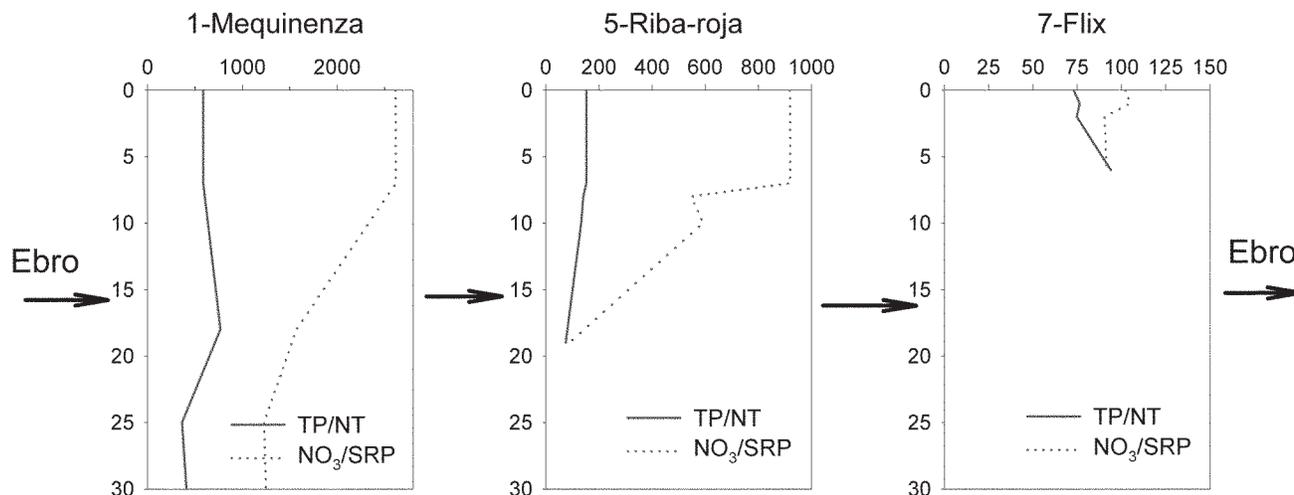
Figure 5.-N:P ratio profiles at the three study reservoirs (Mequinenza, Riba-Roja and Flix). Solid lines show ratios of total nitrogen and total phosphorus, while dashed lines are ratios of soluble fractions. The direction of water flow is shown by the arrows between panels.

densities decreasing from 30 to 11 and 8 ind l^{-1} at stations 5, 6 and 7, respectively. The rope extraction took place one week before the rest of the sampling (after five weeks of colonization). At 10 days, the rope had small zebra mussels attached at 2 m below the surface. After five weeks, the entire length of rope was colonized. There were two distinct mussel density peaks down the rope length (Fig. 6B). A maximum density was found near the 3 m depth, while the main aggregation of animals was at 12 m The maximum density of individuals (ind m^{-1}) was found in the hypolimnion (Fig. 6B), while maximum mean weight was near the surface, between 0 and 5 m (Fig. 6C). The vertical distribution of animal densities in reservoir basins showed a similar pattern of size and abundance distribution to that on the experimental rope (Fig. 6E, 6F, 6G). Specimen size near the surface was about 4 times larger than nearer the bottom (*i.e.*, a mean of 0.81 g compared to 0.23 g in top and bottom waters, respectively), both on ropes and in the reservoir basin.

Discussion

The distribution of individual mussel weights on the rope (Fig. 6C) and in the reservoir basin of Riba-Roja (Fig. 6F) showed similar patterns. The agreement in size distribution suggests that animal populations in the basin and on the rope had probably been exposed to similar environmental conditions that largely determine adult size (Allen *et al.* 1999, Chase and Bailey 1999, Horvath and Lamberti 1999b). However, maximum animal density on the rope near the Riba-Roja dam occurred at 12 m depth (Fig. 6B), coinciding with the depth of the floodgates of the reservoir. The turbulence generated during the operation of the floodgates could have positively influenced the colonization of animals.

As pointed out by Eyster and Pechenik (1987) and Wacker and von Elert (2003), the attachment of mussel larvae can be facilitated by high water flow because it probably increases the frequency of contact between organisms and substrata. Feeding may also be favoured by flow (Archambault *et al.* 1999). Thus, hydrodynamics could explain the occurrence of mussel colonization at certain depths over others.

Attached larvae in epilimnetic waters may have experienced an optimal combination of factors: temperature, oxygen, hydrodynamics and food (O'Neill 1996). In the epilimnion, pH values (7.69-8.16) are within the optimal-range values (8-8.5) for the development of *Dreissena polymorpha* veligers (Bachmann *et al.* 2001) as well as for zebra mussel adults (Sprung 1987, Ramcharan *et al.* 1992, Bowman and Bailey 1998, Bachmann *et al.* 2001). Alkalinity and carbonates (163 mg l^{-1} CaCO$_3$) were clearly above the limiting concentration for zebra mussel growth (17.1 mg l^{-1} CaCO$_3$; Hincks and Mackie 1997). In addition, oxygen concentration was above the growth inhibition threshold of 2 mg l^{-1} (Heath 1993, Mihuc *et al.* 1999). Food (*i.e.*, phytoplankton) concentration was higher here than at all other sampling stations.

The larger retention time in Mequinenza reservoir (Table 1) could facilitate phosphorus uptake by the algae. The high water temperatures (28.9°C at 1 m), pH (>8.3 from 0 to 4 m) and alkalinity (see Table 1) could enhance the chemical precipitation of phosphorus in the form of apatite (Baccini 1985, Stumm and Morgan 1996). As a result of these processes, water draining into Riba-Roja was phosphorus-poor (station 1 SRP; Fig. 4, top left panel). Phosphate concentrations were around 10^{-7} M, and all N:P ratios were >16, leading us to conclude that P was the limiting nutrient in these reservoir (Reynolds 1997). However, bottom water in Riba-Roja had
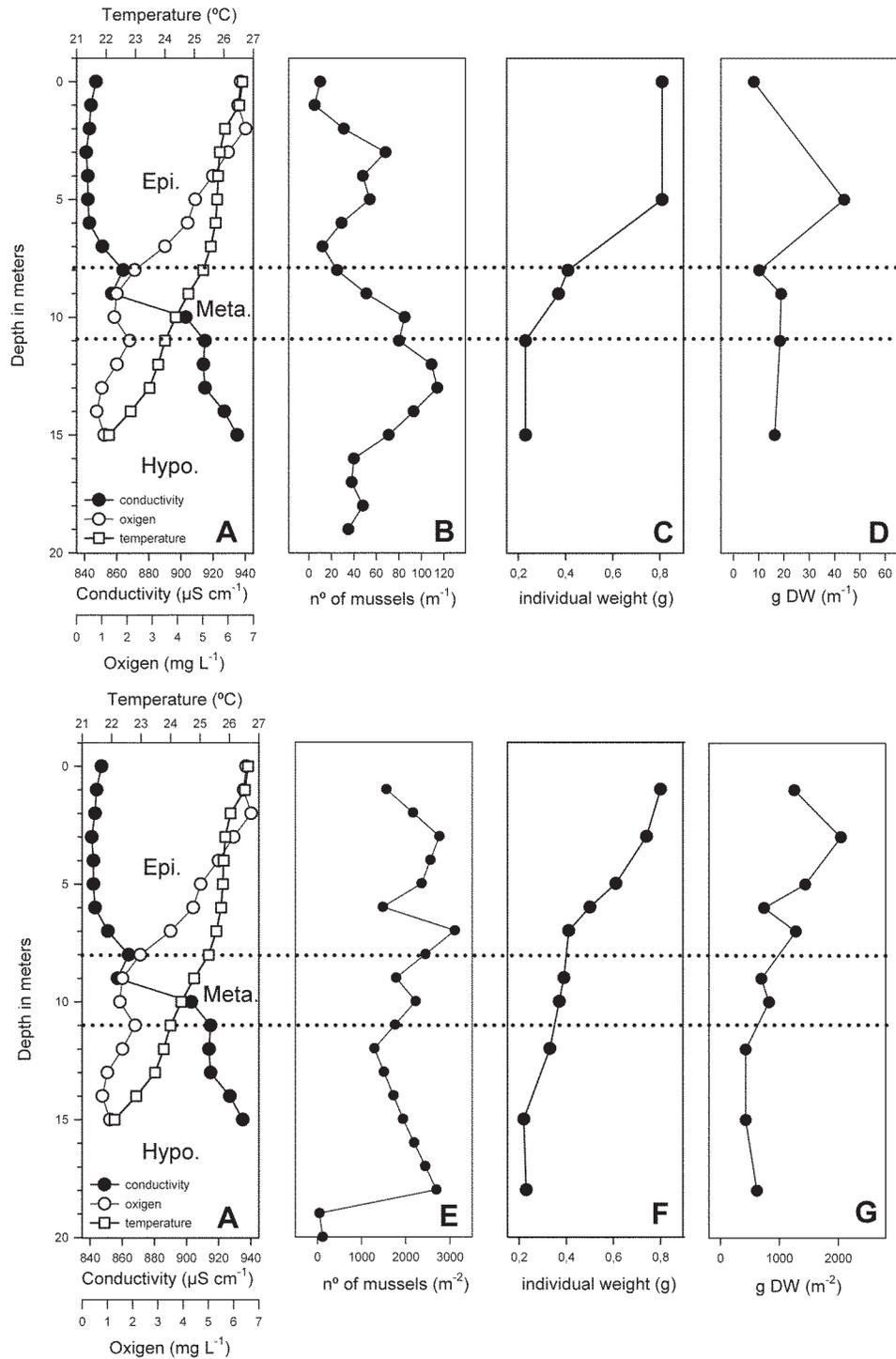
Figure 6.-Temperature, conductivity and oxygen vertical profiles (A) at sampling station 5. Values of conductivity defined three distinct compartments down the water column: epilimnion, metalimnion and hypolimnion. Also shown are the distribution of zebra mussel densities (ind m^{-1}), mean individual weights (g) and biomass (gDW m^{-1}) on experimental colonization rope (B, C and D, respectively) and in the basin (E, F and G, respectively). In the case of figures E and G the units are expressed per m^{-2}.

Table 2.-Relevant regression and correlation values, between oxygen concentration and mussel individual weight and biomass in both, the basin and the rope. Units used in the regression were mg l⁻¹ for the oxygen, and averaged g of individual wet-weight in each linear m of rope or in any square m of basin. For biomass, g dry-weight was used.

	R	R^2	Adjusted R^2	df Model	df Residual	t	p
Individual weight in basin	0.93	0.87	0.83	1	4	5.12	0.0069
Individual weight in rope	0.96	0.91	0.90	1	7	8.58	0.0001
Biomass in basin	0.12	0.01	-0.23	1	4	0.24	0.8244
Biomass in rope	0.84	0.71	0.67	1	7	4.17	0.0042

higher SRP levels (2.28 µM), in contrast with the low levels measured in surface waters (0.9 µM). This pattern of bottom enrichment could partly arise from precipitation of materials carried in from the Segre River, via chemical precipitation (especially for TP). This process could have been enhanced by the longer retention times of water in the epilimnion of Riba-Roja (85 days). Also, the high epilimnetic biomass of zebra mussels (Fig. 6D and 6G) could act as an important vector for nutrient recycling through their excretion, which could be used for primary production (Mellina *et al.* 1995).

Larvae attached to substrata at the greater depths with lower temperatures, lower oxygen levels and less food consequently show lower individual weight (Fig. 6C-F). Oxygen concentrations had a relevant impact on zebra mussel weight. The similarity between vertical patterns of dissolved oxygen concentrations (Fig 6A) and individual mean weights (Fig. 6C-F) could thus be explained by the positive effect of larger oxygen availability on growth in mussel physiology. To test the relationship between oxygen and individual weights and oxygen and biomass in basin and in the rope (Fig. 6A and 6F), linear regressions were performed (Table 2). The significantly high values of the correlation coefficients (R) show that individual weight, and consequently mussel physiology, in basin and rope have a strong dependence on oxygen availability. Biomass accrual in rope also shows a strong correlation with oxygen (Table 2) due to the stability of the environmental conditions during the colonization period. In contrast, the basin biomass is the result of growth during several months, thus integrating different environmental conditions. This integration of different zebra mussel optimal growth depths results in a lack of correlation between the actual oxygen profile and biomass (Table 2).

Oxygen concentrations in the meta- and hypolimnion were <2 mg l⁻¹, which is a known critical level for zebra mussel growth (Mihuc *et al.* 1999). Under these low oxygen concentrations mussels could experience impaired growth (Heath 1993, Karatayev *et al.* 1998, Mihuc *et al.* 1999), and lower mean weights were consistently observed at these depths (see Fig. 6C-F). The high densities of individuals within the hypolimnion (Fig. 6B and 6E) might seem contradictory but

could be due to the sedimentation. In spite of the abundance of hypolimnetic individuals (Fig. 6B-E), their contribution to the total biomass is less important than those growing in the epilimnion (Fig. 6D-G).

Conditions prevailing in the penstock and turbines of Riba-Roja hydropower plant had the potential to negatively affect the viability of larvae. The exposure of the spring zebra mussel veligers to harsh hydrodynamic conditions may have increased their mortality (Horvath and Lamberti 1999a). This would explain the fall in larvae densities from 30 larvae l⁻¹ at station 5 (upstream dam) to 11 larvae l⁻¹ at station 6 (downstream dam).

We conclude that optimal epilimnetic conditions for zebra mussel growth were provided by the stratification of water masses in Riba-Roja reservoir. Distribution patterns of zebra mussels seem to be dominated by the hydrodynamics and thermal stratification of water layers, whereas their growth seems to be controlled by oxygen availability. Stratification in the study reservoirs was the result of the interaction between inflows to the reservoir with distinct physic-chemical characteristics and management practices of the reservoirs. Our results suggest an interesting way to control zebra mussel populations in these systems. In some reservoirs it may be possible to release water from different depths, altering the stratification pattern of water masses, and thus the depth of the epilimnion and hypolimnion water layers. Therefore, with appropriate management of the reservoirs, it may be possible to increase or reduce the volume of water layers where zebra mussel populations find optimal conditions for successful growth and development. More research must be done to determine whether the reservoir's strong seasonality affects mussel populations and settlement during the rest of the year.

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