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SANTA ROSALIA 50 YEARS ON

On non-Eltonian methods of hunting Cladocera, or impacts of the introduction of planktivorous fish on zooplankton composition and clear-water phase occurrence in a Mediterranean reservoir

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Abstract Among the topics covered by Hutchinson's Santa Rosalia article, the question of the shortening and lengthening of food webs occupies a central role. As Hutchinson realized, at the time scales of ecological studies, the impact of invader species on established food webs is the fastest shortcut to the shortening or lengthening of the food webs. The construction of thousands of dams in Spain during the last century has offered ecologists a good opportunity to test the effects of invader fish species on the plankton dynamics of these systems. In this article, a series of data related to the food web structure of Sau Reservoir is analyzed for the period 1997–2005. Parameters such as Secchi depth and chlorophyll concentration, as well as abundance and size structure of zooplankton, have been matched to the zooplankton dynamics in the reservoir. Most of the changes detected within this period are attributed to the introduction of zooplanktivorous fish in the reservoir. The Secchi depth measurements have showed a progressive diminution in the clear-water phase during recent years. These changes have been related to the decrease in the abundance of *Daphnia* and to the reduction of the size of zooplankton, which help to explain concomitant increases in the chlorophyll concentration in the same period. Other observed changes in the composition of the zooplankton community have been the substitution of *Daphnia* by *Bosmina* and the increase in the abundance of rotifers. Thus, the annual average abundance of *Bosmina* in 1997 was 70% of cladocerans, while in 2005 it reached 98%. In parallel, the percentage occurrence of individual rotifers was 40% of total zooplankton numbers but had risen to 85% at the end of the period. All these changes are attributed to the artificial expansion of the food web through stocking of the reservoir with zooplanktivorous fish (*Rutilus rutilus* and *Alburnus alburnus*). This study improves our understanding of the trophic relationships in the food web prior to the introduction of the fish.

Guest editors: L. Naselli-Flores & G. Rossetti / Fifty years after the "Homage to Santa Rosalia": Old and new paradigms on biodiversity in aquatic ecosystems

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Introduction

> A lengthening [of food chains] can presumably occur most simply by the development of a new terminal carnivore link, as its niche is by definition previously empty. (Hutchinson, 1959).

Undoubtedly, *Homage to Santa Rosalia* (Hutchinson, 1959) has become a landmark work in the field of limnology. To date, 1,414 articles cited this work in more than 100 different journals, mainly in the fields of ecology, evolutionary biology, and zoology, but also in freshwater research. While many of Hutchinson's deliberations did not appear exclusively in his article, he might be credited with having brought order to the discipline by stressing the fundamental role of energy in food chains, available habitat and community stability, and how all this relates to biodiversity.

Among the topics covered by the Santa Rosalia article, the question of the shortening and lengthening of food webs is a recurrent theme. However, the appearance of new "evolutionary actors" in the "ecological theatre" is a very rare event, at least at the time-scale of ecological studies. With his celebrated insight, Hutchinson soon realized that the question of the success and impact of invader species on established food webs offered the fastest shortcut to the issue, and it is not surprising that he should have welcomed Elton's book on animal and plant invasions (Elton, 1958), recognizing that it would become a foundation work of research in ecology on species invasions.

There is a general consensus that plankton communities are hardly stable and maintain a relatively high diversity because of frequent external perturbations and complex species interactions, which maintain the community far from equilibrium (Scheffer et al., 2003). From a theoretical point of view, the probability of an "evolutionary event" enlarging a food web by the appearance of a new top predator link is greater in these unstable systems. Fortunately for ecologists, though not for ecosystems, there are many non-Eltonian ways (*sensu* Hutchinson) of enlarging food webs with new top predator links.

The construction of thousands of reservoirs in Spain during the second half of the twentieth century has offered to ecologists a good opportunity to test hypotheses about plankton community assembly and maturation (Margalef et al., 1976). Most phytoplankton and zooplankton groups rapidly became established in these systems, as a consequence of the same efficient dispersal ability that underpins their ubiquitous distributions (Armengol, 1978; de Manuel, 2000). However, lowland lentic systems were once a very rare landscape feature in Spain, prior to the construction of reservoirs, and autochthonous freshwater planktivorous fishes were scarcely present before that. As a result, many Spanish reservoirs still lack any fish predator in the pelagic food web. However, reservoirs that have been stocked with planktivorous fishes (e.g., *Alburnus alburnus*) to provide recreational fishing are sometimes stocked also with a superior predator (e.g., *Silurus* sp.).

The effects of introducing a new predator in a plankton community are numerous, including changes in resources availability, species diversity, or food web topology. The variability in abundance and body size of large-bodied zooplankton, such as *Daphnia*, under the presence of zooplanktivorous fish, is a classical topic in limnology (Hrbácek et al., 1961). Brooks & Dodson (1965) demonstrated early on that in the presence of zooplanktivorous fish the population of large-bodied filterers is eliminated and replaced by small-bodied zooplankton, basically *Bosmina*. However, the introduction of zooplanktivorous fish also modifies the emergent properties of the ecosystem such as the duration and intensity of clear-water phases (Luecke et al., 1990). Within a short period of time, normally in spring, an episode of rapid phytoplankton growth is followed by one of in which it is abruptly eliminated, precipitating a distinct period of clear water (Sommer et al., 1986). This phenomenon, known as clear-water phase, coincides with a spring peak in the abundance of a zooplankton that comprises many large-sized cladocerans (Lampert et al., 1986). Zooplankton continuously filters particles in the range of 1–10 μm, mainly algae, bacteria, and detritus or organic aggregates, which may greatly attenuate light (Stemberger & Miller, 2003; O'Sullivan & Reynolds, 2005). The capacity of zooplankton filtration is related to its body size, so the larger the animal, the greater its capacity of filtration and the range of particle size it can capture. The relationship between body size and filtering efficiency was first observed by Brooks & Dodson (1965), who established the size–efficiency hypothesis. Biomanipulation experiments have demonstrated that the development of phytoplankton is weaker in the presence of large-bodied zooplankton (e.g., *Daphnia),* but not so when small cladoceran or rotifer species (Carpenter & Kitchell, 1993) dominate. In its turn, extensive empirical data suggest a major role for cladoceran body size on chlorophyll and water transparency levels (Stemberger & Miller, 2003). Many mesocosm experiments suggest that fish predation, mediated by visual feeding on large-bodied filter-feeders, promotes top-down effects on phytoplankton communities and on water transparency (Wright & Shapiro, 1984; Gliwizc, 1990; Gliwizc & Boavida, 1996; Angeler et al., 2002; Benndorf et al., 2002; Chase, 2003; Kwang-Hyeon et al., 2004; Steiner, 2004).

In this study, we want to show the consequences of artificially enlarging the food web of a pelagic community by adding a zooplanktivorous fish to a Spanish reservoir, using data from 1997 to 2005. We focused mainly on investigating whether the mean size of zooplankton is associated with attributes likely affected by bottom-up or top-down effects: variability in chlorophyll *a*, phosphorus concentration, and modifications in the dynamics of clear-water phases.

Materials and methods

Study site

Sau Reservoir is located in the northeast of Spain. It was built in 1963 to serve multiple purposes: hydroelectric power generation, agricultural watering, domestic and industrial water supply, and to provide recreational activities (Vidal & Om, 1993). These include the fishing that has become an important activity during recent years.

Sau Reservoir is a long, canyon-shaped, deep reservoir (Table 1), with a maximum length of 18 km. Its main tributary, the Ter River, has a very irregular flow, which is a typical feature of Mediterranean rivers. The discharges of the river to the reservoir can vary from 2 $m^3 s^{-1}$ to less frequent values of 2000 $m^3 s^{-1}$, with an average value of 18 $m^3 s^{-1}$. The catchment area is 1,790 km^2 and main land uses are forestry, arable agriculture and urbanisation (Vidal & Om, 1993).

Table 1 Main morphometric and hydrological features of Sau Reservoir

Parameter	Value
Location	46°46′N, 4°51′E
Altitude (m.a.s.l)	362
Maximum volume (10^6 m^3)	168.5
Maximum area (10^6 m^2)	5.8
Maximum depth (m)	65.0
Mean depth (m)	25.2
Mean length (10^3 m)	18
Mean width (10^3 m)	1.3
Mean inflow (10^6 m^3 $year^{-1}$)	540.5
Mean residence time (years)	0.26

The trophic state of Sau Reservoir has changed remarkably through time. During its first four decades, the reservoir suffered an acute process of eutrophication. However, after the construction of tertiary sewage treatment plants in the most important towns in the upper basin of the Ter River during the early 1990s, the nutrient load decreased considerably (Armengol et al., 1986; Vidal & Om, 1993; Armengol et al., 1999; Marcé et al., 2004). Nowadays, Sau Reservoir varies between eutrophic and mesotrophic states.

The abundance and dynamics of the zooplankton community in Sau Reservoir have been followed as a part of a long-term water quality monitoring program. So far, 48 species of zooplankton have been identified. A total of 33 species of rotifers, 3 of copepods, and 9 of cladocerans have been found. Approximately 20% of the total individuals are represented by *Keratella cochlearis*, 17% by *Polyarthra major*, and 12% by *Bosmima longirostris*. *Daphnia galeata* is the most abundant large-bodied cladoceran.

The fish population in Sau Reservoir is dominated by *Alburnus alburnus*, *Cyprinus carpio*, *Rutilus rutilus*, and *Barbus graellsii* (Table 2). The presence of *Silurus glanis* has also been reported. All except *B. graellsii,* are introduced species. Data from 2004 (E. García-Berthou, personal communication) suggest a fresh biomass of fish of around 600 metric tons, with a

Table 2 Fish abundance estimated with multi-mesh gillnets (Carol et al., 2006)

Fish species	CPUE[a]
Alburnus alburnus	1.166
Cyprinus carpio	0.517
Rutilus rutilus	0.697
Barbus graellsii	0.068

[a] *CPUE* catch per unit effort

high predominance of *A. alburnus*. *Silurus* was introduced in the reservoir for recreational fishing sport, since it is a large-sized fish that is attractive to anglers; it was introduced together with other species to provide its food base (mainly *A. alburnus*). There are no estimates of abundance or density of *Silurus* in the reservoir, but specimens of approximately 6 years old were captured in 2004. Judging by the kind of fishing prevalent (put-and-take fisheries), it is likely that these fish were stocked during 1999.

Zooplankton sampling and counting

Data in this study correspond to monthly samples taken between 1997 and 2005. All the data were taken at a station situated at 500 m from the dam to avoid the turbulence effects produced by the outlet and the wind blowing against the dam. The zooplankton was collected through vertical hauls from 20 m depth to the surface, using an Apstein net with 53 µm mesh. Samples were anesthetized with CO_2-charged water and preserved with a sucrose–formalin solution. Once in the laboratory, the samples were sieved through a sieve series of mesh sizes, 750, 500, 250, 150, 100, and 53 µm, with the aim of separating and simplifying the identification and counting of the organisms.

Identification and counting of zooplankton was performed in an Utermöhl chamber with an inverted microscope, counting a minimum of 60 individuals of the most abundant species (McCauley, 1984). Biomass of each species was determined from the conversion of length measurements using different geometric formulations and length–weight relationships (Dumont et al., 1975; Bottrell et al., 1976; Ruttner-Kolisko, 1977; Malley et al., 1989).

Chemical analyses

Water samples were taken at selected depths using a 5-l hydrographic bottle; however, in this study, we used only data integrated over the uppermost 10 m. The parameters taken into account were total-phosphorus concentration (TP), total load phosphorus from the Ter River (TP_{load}), chlorophyll *a* (Chl-*a*), and suspended solids (SS). Secchi depth (SD) was measured as an estimator of water transparency.

For determination of chlorophyll and suspended solids, a known volume of water was filtered through WHATMAN GF/F glass microfiber filters. The concentration of total suspended solids was obtained from the difference in weight of the filter before and after filtration. The concentration of inorganic suspended solids was obtained from the difference in weight of the filter before and after burning at 450°C during 4 h (APHA, 1992). The chlorophyll *a* content of phytoplankton was analyzed by the trichromatic method of Jeffrey and Humphrey (1975). The phosphorus concentration was determined by acid-digestion, following the method proposed by Murphy & Riley (1962). Phosphorus load from the Ter River was obtained from Marcé et al. (2004).

Statistical analyses

A path analysis was used for estimating the direct and indirect effects on the water transparency of the variables studied during the clear-water phase. This analysis is an extension of the linear regression model, in which the correlation coefficient of the relationship between the dependent and the independent variables is partitioned into direct and indirect effects through other independent variables (Sokal & Rolf, 1995; Legendre & Legendre, 1998). To accomplish the path analysis, a priori hypothetical relationships between criterion (dependent) variables and predictor (independent) variables are defined. Arrows in the resulting diagram (path diagram) indicate causation between two variables. The value over the arrows is the path coefficient, which is the standardized regression coefficient or beta coefficient, and shows the direct effect of an independent variable on a dependent variable in the path model. The final value of each path is the product of its path coefficients. And the sum of such products is the indirect effect of a predictor variable on a criterion variable.

It is not possible to test the model obtained from the path analysis. The chi-squared or Z tests require a longer data set. Therefore, the strength of the direct and indirect effect of the different variables on the Secchi-disk depth was inferred in a non-statistical manner from the amount of each coefficient and the sign. The main goal of this analysis was to corroborate the importance of zooplankton size on water transparency as compared to other variables.

Results

During the period 1997–2005, rotifers were generally the most abundant group, followed by cladocerans and copepods (Fig. 1A). In 1997, the total abundance of zooplankton was composed mainly of rotifers, almost 90%. Between this year and 2000, the percentage of rotifers decreased. By contrast, cladocerans and copepods increased; cladocerans increased most. By 2000, the percentage of cladocerans was greater than 40%, followed by rotifers with a percentage smaller than 40% and finally the copepods, albeit with an increased percentage of 12%. From 2001 on, the population abundance of cladocerans decreased dramatically to a value that hardly exceeded 10%. Meanwhile, rotifers reached more than 85% of the total. In terms of biomass, the community was dominated by Cladocera during the early years. Since then, there was a dramatic decrease in Cladocera biomass, which was substituted by copepods (Fig. 1B). The decrease in *Daphnia* since 2002 is matched by the increase of rotifer abundance and species richness (Fig. 2).

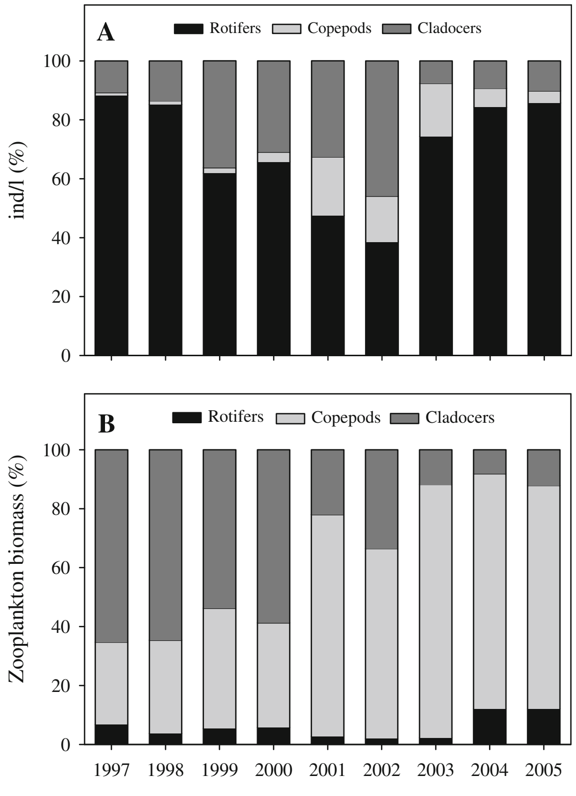


Fig. 1 Temporal variability of zooplankton abundance (**A**) and zooplankton biomass (**B**) in Sau Reservoir from 1997 to 2005

The average size of cladocerans in 1997 was 0.51 mm, with a community distributed in three main size classes (Fig. 3). The first of these, between 0.3 and 0.5 mm, and in which most of the cladocerans occurred, comprised mainly *Bosmina*, with some individuals of the *Ceriodaphnia* and *Moina* genera. The next size class, 0.6–0.7 mm, including mainly individuals of the *Moina* genus, exhibited an abundance close to 8%. And the last two size classes, 0.7–0.8 and <1 mm, consisting of individuals of *Daphnia* and *Diaphanosoma* genera, exhibited an abundance of approximately 20%. We found a very different scenario 8 years later. The mean size for the Cladocera was 0.37 mm in 2005, a decrease of almost 30% in body size as compared to 1997. Also, a substantial change in the abundance distribution of cladocerans for the same three classes had occurred. Practically 98% of the population was included in the 0.3–0.5 size class, the smallest one, and comprised almost wholly individuals of *Bosmina* (Fig. 3). This means that *Daphnia* and *Diaphanosoma* almost disappeared.

Dividing the population dynamics of *Daphnia* genus in three inclusive time periods (viz. 1997–2001, 2001–2003, and 2004–2005; see Fig. 4), it may be observed that in the first period there were two growth peaks, one during the spring, in March, and the other in June, just starting the summer station. In the second period of time, the first growth peak remained but the second decreased considerably. And eventually, in the last period of time, *Daphnia* disappeared almost completely.

Mean Secchi depth was very irregular but tended to decrease between 1997 and 2005 (Fig. 5). During this period, Secchi depth decreased almost 1 m, from

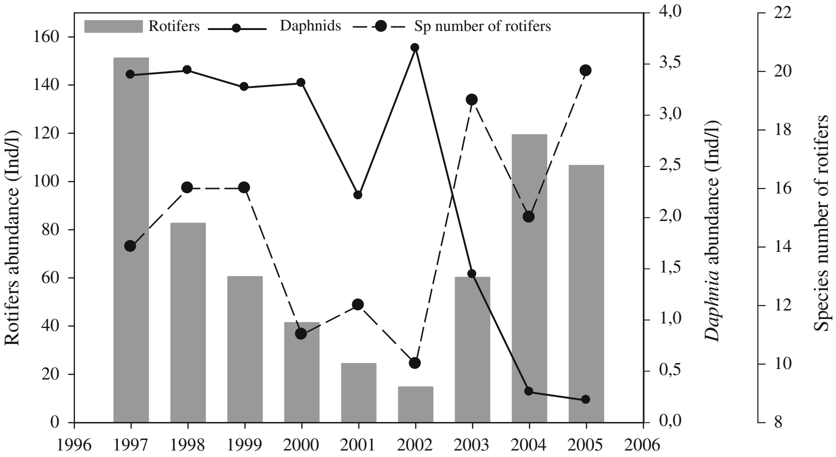


Fig. 2 Rotifer abundance and species number variability, as compared to *Daphnia* abundance and variability in Sau Reservoir

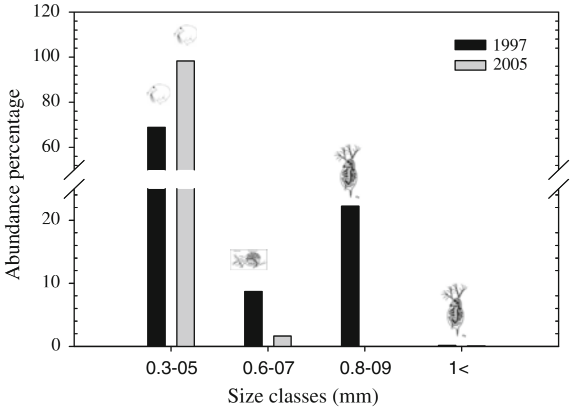


Fig. 3 Relative abundance of cladoceran body size classes in Sau Reservoir during the period 1997–2005

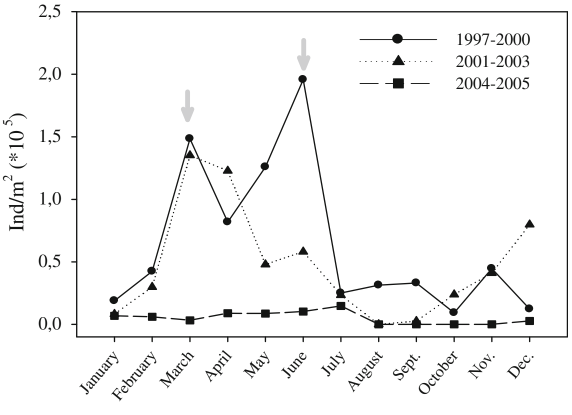


Fig. 4 Temporal dynamics of *Daphnia* in Sau Reservoir between 1997 and 2005. The *arrows* indicate the growth peaks of the genus in the period 1997–2000

2.84 to 1.90 m. The maximum values were observed in January and February of 2003 with 6.64 and 5.60 m, respectively. These high Secchi measurements coincided with the minimum mean values of suspended solids through the entire series. The minimum Secchi-disk depth was obtained in March 2001, coinciding with the maximum observed values of suspended solids. Until 2003, the clear-water phase occurred between the second and the fourth month of each year in a quite constant manner (Fig. 5). In subsequent years, the clear phase diminished in duration and intensity. In 1999, there was no clear-water phase either and the water transparency was the lowest of the series, coinciding with high values of suspended solids related to low water volume. During this year, the volume did not exceed 54 hm^3, and the average value for the series was 117.28 hm^3.

The mean monthly total-phosphorus concentration (1997–2005) and the chlorophyll concentration were positively and significantly correlated (Fig. 6A). So were the chlorophyll concentration with zooplankton abundance (Fig. 6B) and suspended solids with Secchi depth (Fig. 6C).

During the clear-water phase, the chlorophyll concentration and the mean size of cladocerans (CMS) in Sau Reservoir showed an inverse trend, almost throughout the entire data series (Fig. 6D). The corresponding correlation is inverse and significant. In contrast, the trend shown by the Secchi depth and the cladoceran body size is almost the same throughout the data series, therefore the correlation was positive and significant (Fig. 6E). Table 3 summarizes the correlations obtained among the variables investigated.

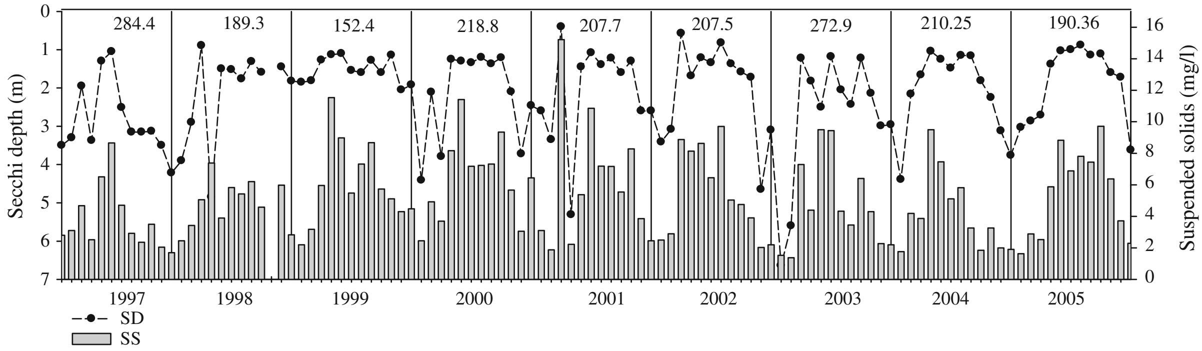
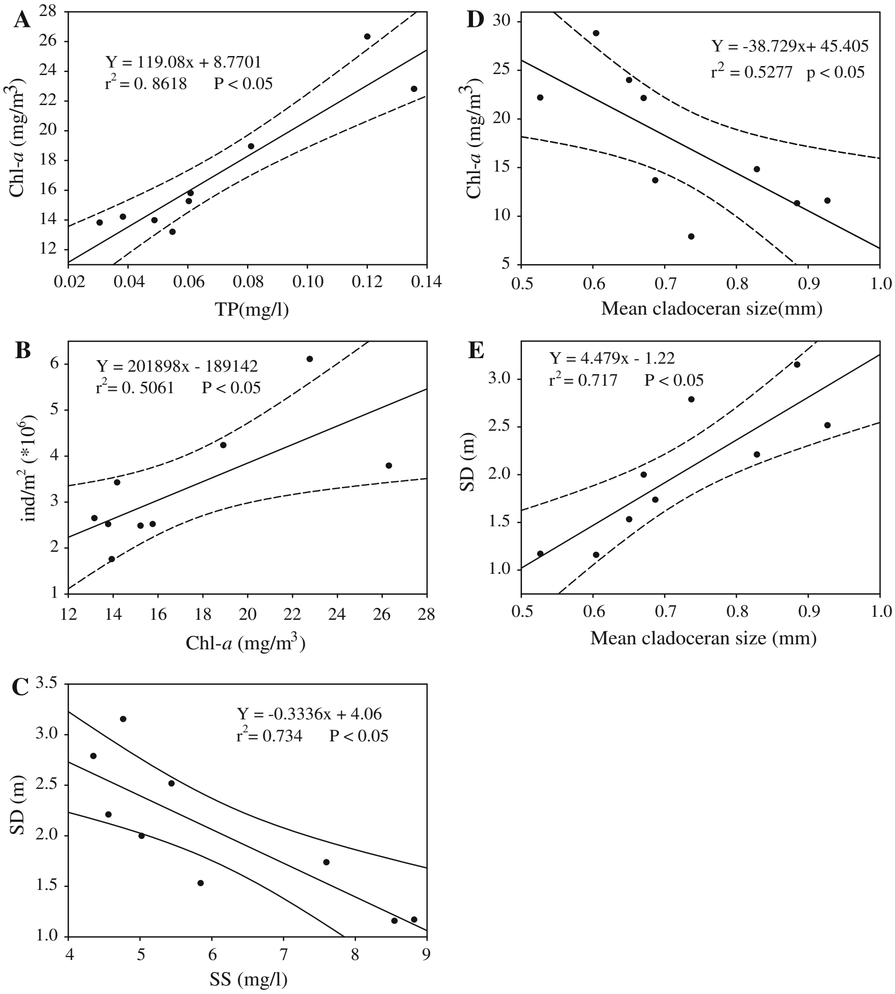


Fig. 5 Water transparency (SD) and suspended solids (SS) variability in Sau Reservoir during the period 1997–2005

Fig. 6 Relationship between total-phosphorus and chlorophyll *a* concentration (**A**), chlorophyll *a* concentration and zooplankton abundance (**B**), Secchi depth and suspended solids (**C**), chlorophyll *a* concentration and mean cladoceran body size, during the clear-water phase (**D**), and Secchi depth and mean cladoceran body size, also during the clear-water phase (**E**)



The path analysis suggested that zooplankton size and chlorophyll concentration were the main drivers of Secchi depth (Fig. 7). The resulting correlation coefficients estimated for the different possible paths are showed in Table 4. From the whole analysis, zooplankton body size (ZS) was the variable that indirectly contributed the most to Secchi depth, via chlorophyll concentration.

Table 3 Selected correlations between variables during the clear-water phase in Sau Reservoir

	Chl	SD	CMS	SS_i	RT	TP_{load}
Chl	1.00					
SD	**−0.85**	1.00				
CMS	**−0.73**	**0.85**	1.00			
SS_i	0.28	−0.41	−0.39	1.00		
RT	−0.31	0.34	0.65	−0.42	1.00	
TP_{load}	0.23	−0.29	−0.12	0.48	−0.44	1.00

Significant values ($P < 0.05$) are shown in bold case. *RT* water residence time, *CMS* cladoceran mean size

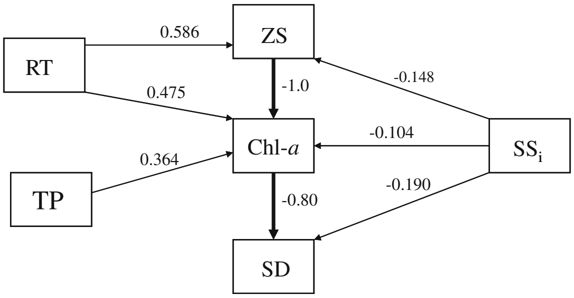


Fig. 7 Path analysis diagram. The *arrows* show causation between two variables and the number over them the strength of the relationship between those variables (*RT* water residence time, *ZS* zooplankton mean size, *SD* Secchi depth, *TP* total-phosphorus, *SSi* inorganic suspended solids, Chl-*a* chlorophyll *a* concentration)

Table 4 Summary of path coefficients for every possible causal link between the selected explanatory variables and Secchi depth

Path	Path coefficient	Aggregated path	Aggregated path coefficient
RT → ZS → Chl-*a* → SD	0.47		
RT → Chl-*a* → SD	−0.38	RT → SD	0.09
TP → Chl-*a* → SD	−0.29	TP → SD	−0.29
SS_i → ZS → Chl-*a* → SD	−0.12		
SS_i → Chl-*a* → SD	0.08		
SS_i → SD	−0.19	SS_i → SD	−0.23
ZS → Chl-*a* → SD	0.80	ZS → SD	0.80

RT water residence time, *ZS* zooplankton size

Discussion and conclusions

Zooplankton size was the variable contributing the most to water transparency variability during the clear-water phase in Sau Reservoir. The Secchi depth, as a measure of water transparency, was positively related to zooplankton size; however, this is an indirect relationship because the chlorophyll concentration is the variable that really affects water transparency, which is also affected by the existing relationship with zooplankton size. All these relationships are included in the conceptual framework of the body size–efficiency hypothesis (Brooks & Dodson, 1965). Observing the path diagram, one can see the direct and indirect relationships more clearly. The diagram shows the strength of the indirect effect, is like that of zooplankton body size on water transparency, linked through grazing of the algae. In other words, variations in the effect of large zooplankton on chlorophyll concentration are responsible for the variability in Secchi-disk depth. This grazing pressure exerted by zooplankton filter-feeders on the algal stock and its unleashed effects on lower trophic levels may be defined as a top-down process. This also explains why the variance in phytoplankton biomass is less well related to the variability in nutrient concentration (Thornton et al., 1990).

Daphnia, linked to the normal occurrence of a clear-water phase, suffered a sharp decrease in abundance of the populations that were attained after 2002. The mean body size of cladocerans fell remarkably between the beginning and the end of the series, declining from 0.51 mm in 1997 to 0.37 mm in 2005. These changes could be related to the clear-water phase disappearance during the last 2 years of the data series, caused by the low filter rate of the smaller zooplankton.

Analyzing average data from Sau Reservoir obtained between 1995 and 2001, Armengol et al. (2003) concluded that chlorophyll concentration is not as good a predictor of water transparency as is the concentration of suspended solids. Sau Reservoir contains abundant sediment transported in suspension in the Ter river inflows and also from the shore as a consequence of water-level variability. These conclusions are true but it must be emphasized that, in these results, total suspended solids correspond to the sum of all the particles present in water, including algae.

When relating the inorganic fraction of the total suspended solids (SSi) with Secchi-disk depth during the clear-water phase, avoiding the covariance between chlorophyll concentration and total suspended solids (SS), a low contribution of this fraction on water transparency could be observed, although there was some relationship. Meanwhile the relationship between zooplankton body size and chlorophyll with water transparency was higher in both cases.

Neither residence time nor the river-borne phosphorus loadings contributed significantly to water transparency during the clear-water phase. Ter river phosphorus load has been related to eutrophication processes in Sau Reservoir and, hence, its algal production (Armengol et al., 1986; Vidal & Om, 1993; Armengol et al., 1999; Comerma et al., 2003, Marcé et al., 2004, Feijoó et al., 2008). However, data analyzed in the present research show little impact of phosphorus loadings compared to other predictor variables on water transparency during the clear-water phase. Meanwhile, as was mentioned previously, both zooplankton size and chlorophyll concentration are important contributors.

On the other hand, but in this case with monthly data, a positive and significant relationship between epilimnetic total-phosphorus and chlorophyll concentration was found, as there was between the later and zooplankton abundance. These results suggest a bottom-up process (Carpenter & Kitchell, 1993) in which the primary production variability is determined by the nutrient availability, particularly, in this case, of phosphorus; following the food chain, zooplankton growth is determined ultimately by primary production. So, both bottom-up and top-down processes take place in Sau Reservoir although the second process occurs in Sau only during the clear-water phase. Meanwhile, bottom-up process occur throughout the whole year.

Together with the reduction of *Daphnia* abundance since 2002 and the general decrease in the mean size of individuals, several other changes have occurred in the zooplankton communities of Sau Reservoir. Until 2002, rotifer population abundance had shown decreases opposite to the trends in cladoceran numbers. Rotifer populations are reduced in the presence of *Daphnia* for two reasons. First, the intraspecific competition for resources and its availability: both groups of zooplankters share the same food niche but *Daphnia* feeds on a wider size-spectrum of potential foods and, besides, it does so more efficiently. So when the resources are reduced in any system, normally *Daphnia* will be expected to be more competitive. The second reason is more mechanistic: *Daphnia* can ingest some rotifer species and keep them for a while in its abdominal chamber. Some are expelled in a good condition but others can suffer enough damage to cause their death (Gilbert, 1988).

At the end of 2002, the percentage of cladocerans and rotifers was almost the same and the copepods had suffered a slight increase. However, from that year on the cladoceran community started to decrease considerably as the rotifer community increased. Copepod community stayed almost constant during 2003, but afterward, in 2004, decreased sharply. All these changes coincided with an increase in abundance and species number of rotifers.

In Sau Reservoir, these significant changes in the zooplankton community may be associated with the introduction of exotic fish. The *Silurus* introduction, in approximately 1999, together with the zooplanktivorous fish *A. alburnus* and *R. rutilus*, coincided with several changes in the zooplankton community, especially from 2003 on. Juveniles of these two cyprinid species are zooplanktivorous, as are most juvenile European cyprinids. However, with increasing body size, *R. rutilus* foraging expands to include not only zooplankton (García-Berthou, 1999; Persson & Hansson, 1999; Vašek et al., 2003). *A. alburnus*, however, is a more specialized open water feeder, foraging primarily on zooplankton throughout its entire life (Politou et al., 1993; Herzig, 1994; Vinni et al., 2000). The reduction in cladoceran body size during recent years, and the shift to species smaller than 0.5 mm, basically of the genus *Bosmina*, are consistent with the selective predation strategy of zooplanktivorous fishes, in which there is a preferential removal of larger individuals of larger species. The results here also agree with those obtained by Brooks & Dodson (1965), according to whom *Daphnia* species are more vulnerable and smaller species like *Bosmina* survive more successfully. An increase in filament algae could also inhibit the *Daphnia* development (Steiner, 2004), but during the studied period, no important bloom of these algae occurred.

In the present results, it is evident that there was not just a dramatic decrease in *Daphnia* populations in Sau Reservoir but that the responses could be readily fitted into three time periods, which also fit well to the schedule of introductions of exotic fish. The first growth peak coincided with the maximum algal growth of spring and summer. This leads us to think that the fish introduction had not yet affected the cladoceran population. In the second time period, 2001–2003, first growth peaks analogous to those noted in the three previous years were observed. However, the second growth peaks were considerably smaller, suggesting that the fish introduction had, by then, started to have an effect on *Daphnia*. Finally, in the third time period the *Daphnia* populations had collapsed almost totally, coinciding with the 2 years in which no clear-water phase occurred.

According to the above, it is easy to deduce the top-down effects that fishes have been exerting on the zooplankton communities of Sau, in turn affecting water transparency and, hence, that they have been the main agent of elimination of clear-water phases in the reservoir during the last two years of the data series. It is well known that *Daphnia* populations can generate very large filtering capacities, between 5-80 ml $\mathrm{ind}^{-1}\ \mathrm{d}^{-1}$, and assimilation capacity: a *Daphnia* of 0.8 mm can filter 2.4 μg C d^{-1} (Reynolds, 1984). Thus, its effect on water transparency can be considerable.

All in all, our data reflect the profound changes suffered by a plankton community after the lengthening on the food web with the addition of two vertebrate carnivore levels. Not only were the abundance and composition of the zooplankton community altered but the suppression of features such as a clear-water phase represents a major change to emergent behavior. The outcome is similar to the conclusion reached in many other contexts: when food webs are manipulated in non-Eltonian ways (see page 148 in Hutchinson (1959)), the likely result is a less diverse community with a reduction in the ecosystem services provided by the entire ecosystem. In this case, increased phytoplankton biomass, a consequence of the removal of a key herbivore from the food web, counters the efforts of a water supply company to abstract water of the highest quality from its reservoir. Considering the adaptability of the invasive fishes to the new habitat, the absence of competition and the uninformed attempt to encourage fishing activity in the area, not even her most devoted disciples would think Santa Rosalia capable of solving the problem.

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