Ecology / *Écologie*

Changes in roach (*Rutilus rutilus* L.) population structure induced on draining a large reservoir

*Changements induits par la vidange d'un grand réservoir sur la structure d'une population de gardons (*Rutilus rutilus *L.)*

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Abstract – The influence of draining a large reservoir (Pareloup, South of France) on the population structure and the growth of roach is studied in this work. This reservoir, with an area of 13 km^2, drained in June 1993, was refilled 2 months later. Fish were sampled monthly before draining (1981) and after refilling (1997) by nylon monofilament gill nets used at the same catching effort for both periods. This permitted a comparison to be made between the density of roach and length distribution before and after refilling. Changes in growth were determined by scalimetry. The observed difference in population structure and growth underlined that the differences are mainly due to a greater growth rate after refilling during the first 2 years of roach life. These growth changes are explained by the decrease in roach density and the increase in 1993 of the biomass of zooplankton, which constitute the main feeding resource for 0$^+$ and 1$^+$ roach. The study led us to propose hypotheses on the ecological significance of growth changes induced by refilling, which can be considered as a rejuvenation of the aquatic ecosystem. (© Académie des sciences / Elsevier, Paris.)

roach / draining / gill nets / scalimetry / growth / trophic state

Résumé – Cette étude décrit l'influence de la vidange d'un grand réservoir (lac de Pareloup, France) sur la structure et la croissance d'une population de gardons. Ce réservoir, d'une surface de 13 km^2, vidangé en juin 1993, a été remis en eau après une période d'assec de deux mois. Les poissons ont été échantillonnés mensuellement avant vidange (1981) et après vidange (1997) à l'aide de filets maillants utilisés avec un effort de pêche similaire pour les deux périodes. Cela a permis de comparer les densités de gardon et les distributions de tailles avant et après vidange. Les changements de croissance ont été déterminés par scalimétrie, les différences observées dans la structure en taille et la croissance révèlent une meilleure croissance des gardons durant leurs deux premières années de vie après la vidange. Cette accélération de croissance peut être expliquée par une diminution de la densité de gardon et par une augmentation de la biomasse de zooplancton en 1993 qui constitue la principale source de nourriture des 0$^+$ et 1$^+$. Cette étude a conduit à proposer des hypothèses quant à la signification écologique des changements de croissance induits par la vidange qui peut être considérée comme un rajeunissement de l'écosystème aquatique. (© Académie des sciences / Elsevier, Paris.)

gardon / vidange / filets maillants / scalimétrie / croissance / état trophique

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Le fonctionnement des écosystèmes aquatiques est largement influencé par la structure et la dynamique des populations qui les composent. L'étude de la croissance des poissons en fonction de la qualité de leur environnement a donné lieu à de nombreux travaux. Dans le cadre de cette étude, le suivi de la structure de la population de gardon nous a permis de formuler des hypothèses quant au stade de maturation d'un grand réservoir français après une perturbation anthropique majeure. En effet, le lac de Pareloup a été totalement vidangé en juin 1993 puis remis en eau deux mois plus tard. Cet événement constitue une rupture du continuum évolutif de l'écosystème qui suit habituellement trois phases: une explosion trophique, suivie d'une dépression trophique puis d'une phase de stabilisation.

L'échantillonnage des gardons a été réalisé mensuellement durant 12 mois, en 1981 (avant vidange) et en 1997 (après vidange), à l'aide de filets maillants en nylon monofilament. La batterie de filets utilisée était constituée de six tailles de mailles (10, 14, 17, 21, 26 et 30 mm mesurés nœud à nœud), l'effort de pêche a été analogue durant les deux périodes. Cela a permis de comparer les densités de gardons et les distributions en tailles avant et après vidange sur la base des captures par unité d'effort de pêche (CUEP: captures/100 m^2 de filet/24 h). À partir de la lecture des écailles, la structure en âge de la population de gardons durant les deux périodes considérées a été étudiée. Les longueurs rétrocalculées à l'aide d'un modèle de type puissance ont permis de déterminer la croissance des poissons et de comparer les accroissements standards définis comme étant la moyenne de l'accroissement en longueur des individus de chaque cohorte lors du passage d'un âge donné au suivant. Afin d'éviter un biais induit par la prise en compte des gardons réintroduits suite à la vidange et provenant d'autres milieux, seuls les poissons âgés de moins de cinq ans ont été étudiés pour chacune des deux périodes d'étude. Les gardons âgés de deux ans n'ont pas été pris en compte du fait du faible nombre d'individus capturés avant la vidange. L'étude des poissons âgés de 1 an a été faite sur la base de données issues de pêches électriques réalisées en 1981 et 1997. En effet la taille de ces poissons ne permet pas leur capture à l'aide des mailles utilisées.

Les résultats obtenus révèlent une diminution de la densité de gardon d'environ 13 % par rapport à la situation avant vidange. La comparaison des accroissements standards révèle une différence significative entre les deux périodes étudiées durant la première année de croissance des gardons de 1^+ (test de Mann Whitney, à 1 an $U = 546$ $p < 0{,}001$) et les deux premières années de croissance des gardons de 3^+ (test de Mann Whitney, à 1 an $U = 10$ $p < 0{,}001$, à 2 ans $U = 107$ $p < 0{,}01$) et de 4^+ (test de Mann Whitney, à 1 an $U = 7$ $p < 0{,}001$, à 2 ans $U = 353$ $p < 0{,}001$). L'hétérogénéité constatée entre les deux périodes (avant et après la vidange) provient donc d'une croissance accélérée des poissons durant les deux premières années de leur vie. La croissance avant vidange est proche de celle rencontrée dans différents lacs européens où les populations de gardons font du nanisme. En revanche, les valeurs obtenues en 1997 se révèlent supérieures à celles rencontrées dans ces divers plans d'eau d'Europe de l'Ouest.

La comparaison des températures de surface relevées mensuellement durant les deux périodes étudiées (i.e. 1978–1981 et 1993–1997) ne révèle pas de différence significative (test de Mann Whitney, $U = 797$ $p > 0{,}1$). Le facteur température n'a donc pas un rôle prépondérant dans cette étude.

En revanche, les différences observées peuvent être expliquées par un changement de densité de poissons provoqué par la vidange. En effet, la biomasse totale de poissons avant vidange avait été estimée à 68 $kg \cdot ha^{-1}$ alors qu'après vidange elle atteint seulement 20 $kg \cdot ha^{-1}$. De plus, le nombre de gardons, quatre ans après la vidange, a diminué d'environ 13 %. Le facteur densité est connu pour être largement impliqué dans les phénomènes de croissance individuelle. Celui-ci est intimement lié à la notion de compétition entre individus, notamment vis-à-vis de la disponibilité en ressources alimentaires. Les études menées sur la retenue de Pareloup concernant le régime alimentaire des gardons montrent que le zooplancton constitue la principale ressource alimentaire pour cette espèce durant les deux premières années de vie. Ensuite, plus les gardons vieillissent, plus la part de végétaux et de détritus dans leur régime alimentaire augmente. Suite à la vidange, une explosion de la biomasse zooplanctonique a été observée, ainsi qu'une amélioration de la qualité biochimique du zooplancton. Par conséquent, l'accroissement quantitatif et qualitatif de la principale ressource alimentaire des jeunes gardons explique l'augmentation de croissance des gardons durant leurs deux premières années de vie.

Ces résultats nous autorisent à considérer la structure et la croissance de la population de gardons comme un marqueur de l'état trophique de la retenue. La vidange a transformé un écosystème saturé en un écosystème insaturé propice à la croissance des jeunes poissons. Cet événement a contribué à rajeunir l'écosystème aquatique du réservoir de Pareloup, qui débute une nouvelle phase d'évolution. Suite à la vidange, le lac s'est trouvé dans une phase d'explosion trophique qui tend à favoriser les espèces à fort potentiel adaptatif et à fortes potentialités de croissance. Les jeunes gardons ont profité de cette situation pour optimiser leur prise alimentaire et par conséquent leur taux de croissance. Le rang élevé des poissons dans la chaîne trophique leur permet d'intégrer les variations se produisant dans les niveaux sous-jacents auxquels ils sont directement ou indirectement liés par le bais de relations trophiques. Par conséquent, la croissance des jeunes poissons peut constituer un indicateur précis et facilement mesurable de l'état trophique d'un écosystème aquatique.

1. Introduction

It is now accepted that the function of an ecosystem is widely influenced by the structure and dynamics of the populations which make it up [1]. The study of fish growth offers the system ecologist many opportunities to probe the dynamic balance and states of change in aquatic ecosystems [2]. Growth is an important aspect in the life history of fish and it has been frequently studied since the early 1950s [2, 3]. Since the early 1960s , numerous studies have revealed the importance of the availability of resources, including space, shelter and food, on roach growth [4–6]. Changes in the growth rate following an ecosystem disturbance such as rotenone poisoning were demonstrated by Kempe [7]. These earlier studies, however, did not include population removal by draining. The present study, therefore, aims to deal with this aspect.

In this study, we focused on the population structure and the growth of roach, which is one of the most common fish species in European lowland lakes. Fish catches were performed by electrofishing for the youngest roach and gillnetting. Even though using gillnets can induce some drawbacks, which can be corrected according to the selectivity of the net [8, 9], gillnetting is still a suitable method for fish sampling in large water bodies. Jensen [10] demonstrated that gillnets gave a correct estimation of the proportion of tagged fishes in a perch population, and consequently a correct estimation of the population itself. These assumptions are supported by numerous studies which recommend the use of gillnets for analyses of trends in population dynamics and long-term studies of lake fish populations [11].

Anthropic disturbances, such as fish removal induced by draining and refilling a reservoir, influence the structure and the dynamics of the populations, and especially intra- and inter-population relations in the form of competition, predation or parasitism processes [12]. The draining of a lake constitutes a disruption in the ecosystem evolution continuum which usually follows three different phases: a) a trophic explosion phase with intense development of phytoplankton, zooplankton and benthos; b) a trophic depression phase; and c) a stabilisation phase [13].

Our aim was to compare, on the basis of net catches several years before and after the draining of the reservoir, the density and length distribution of roach. Then, several age classes were studied aiming to determine where any observed growth heterogeneity may lie. Finally, the influence of feeding resource availability and lake maturation stage on roach population was studied.

2. Material and methods

Lake Pareloup is located in southwest France, near the city of Rodez (*figure 1*), it covers an area of 1 350 ha with a volume of about 168·10^6 m^3. The maximum depth is 37 m and the average depth 12.5 m. Lake Pareloup is a warm monomictic lake, which is therefore submitted to summer thermal stratification, with low oxygen content below the thermocline (located at about 10 m depth from early June to mid-September) preventing the fish from colonising deep water during this period. The reservoir was filled for the first time in 1952, and was totally drained in 1962. The last draining occurred in June 1993, and refilling started 2 months later in August 1993.

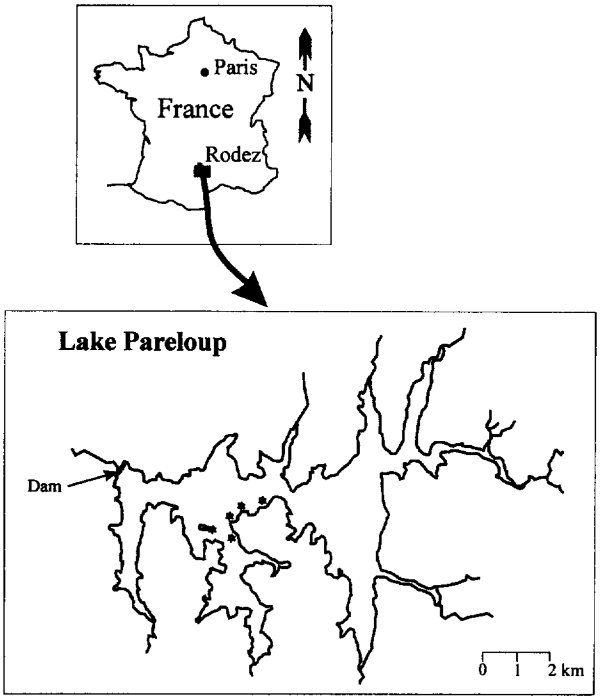

Figure 1. Map of France showing location of Lake Pareloup, stars represent the sampling stations used during the two sampling periods (i.e. before and after draining).

Roach samples were provided by gill net catches performed over two periods using identical sampling design: before draining (i.e. 1981, 19 years after the 1962 draining) and after draining (i.e. 1997, 4 years after the 1993 draining).

Roach captures were performed with nets, 1.6 m high and 20 m long, made of clear, nylon monofilament. Mesh sizes of 10, 14, 17, 21, 26 and 30 mm measured between adjacent knots were used. The monofilament diameter was 0.14 mm. Six nets, one of each mesh size, were set overnight perpendicular to the shore, their sequence was random, and the distance between them was the same, far enough apart for them not to compete for capture of the same fish. A similar effort was used for each 1-year survey; consequently, the number of fish can be compared for each period on the basis of catch per unit effort (CPUE) expressed in catch per 100 m^2 of net per 24 h. Young roach (i.e. 1 year old) were collected by electrofishing in 1981 and 1997. These fish were too small to be sampled by mesh sizes used.

All roach were taken to the laboratory, they were measured to the nearest millimetre (total body length). For ageing purposes, several scales were taken on the left side of each fish, above the lateral line, in front of the dorsal fin. The scales were cleaned by soaking in a 5 % KOH solution before rubbing off the adherent tissues with a small brush. Then, they were rinsed with water and mounted on microscope slides for viewing on a microfiche viewer. A high proportion of regeneration and illegible scales were found and were discarded. Final examination was performed on eight scales for each individual. Scale examination has long been known to be an efficient tool for fish ageing [14]. A detailed histochemical study of the features of roach scales used in ageing has been carried out by Wallin [15]. More recently, many other studies, reviewed by Baglinière et al. [16], have led to the general acceptance of scale reading as a useful technique for ageing fish. All the measurements were made on the same area of the scales as recommended by Boët et al. [17]. The total radius of each scale was measured to determine the best fit between total length and total scale radius. Back calculations were performed using radius measurements between the nucleus and the annuli. From the back-calculated lengths, standard growth was calculated. Standard growth was the mean of the individual length increments per year for all different age groups [7].

To avoid any bias being introduced by roach coming from other ecosystems after filling, only fish under 5 years old were taken into account. Two-year-old roach were removed from the analyses owing to the scarcity of the catches before draining.

Statistical analysis of the data was carried out using SPSS release 7 for Windows, the Statistical Package for the Social Sciences [18]. Non-parametric statistical tests were used to compare the back-calculated growths because of non-normal distribution of the data. Mann-Whitney's U-test was performed to compare the back-calculated length before and after refilling of 1-year-old, 3-year-old and 4-year-old roach. The same test was performed to compare the standard growth increment before and after refilling of 3-year-old and 4-year-old roach. In the same way, water temperatures recorded monthly for the two periods (i.e. 1978–1981 and 1993–1997) were compared using Mann-Whitney's U-test.

3. Results

The comparison of water temperatures for the two periods showed non-significant differences (Mann-Whitney test, U = 797, $p > 0.1$). A more precise season by season comparison (*table I*) revealed no significant differences.

Table I. Median temperature values and results of the Mann-Whitney tests for comparison of the water temperatures between the two periods (1978–1981 and 1993–1997).

Season	Median before draining	Median after refilling	U	p
Winter	3.75	5.00	21.00	0.08 (ns)
Spring	12.25	11.00	47.50	0.65 (ns)
Summer	19.05	18.50	48.50	0.70 (ns)
Autumn	10.15	9.00	48.00	0.70 (ns)

U: Mann-Whitney test value, (ns): not significant at 95 %.

The CPUE revealed a decrease of 13 % in the total number of roach after refilling (*figure 2*). The length distribution shows a difference between the two sampling periods (*figure 2a*) which suggests growth rate variations. Concerning the age structure of the population, *figure 2b* shows a low density of old roach (more than 8 years old) after refilling corresponding to reintroduced adult roach. It was observed that 2, 3, 4 and 5-year-old roach accounted for more than 70 % of the 1997 population. On the contrary, before draining, a low density of 1- and 2-year-old fish were recorded.

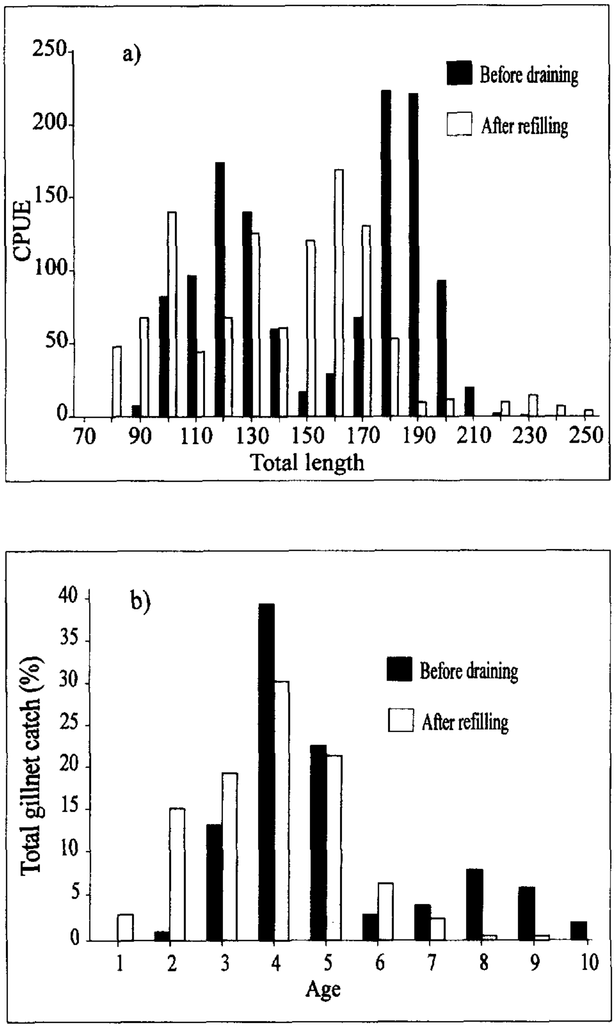

Figure 2. Roach length and age distribution.
a: Length distribution on the basis of CPUE (catch/100 m^2 of net/ 24 h) before and after draining; **b:** age distribution in percentage of total gillnet catch before and after draining.

Back-calculated lengths were used to define the growth of roach before and after the refilling. The best fit between total length (TL) and total scale radius (TR) was obtained, for both periods, by a power model. Equations and determination coefficients were the following:

- before draining: $TL = 3.2687*TR^{0.94}$ $r^2 = 0.90$
- after refilling: $TL = 6.9164*TR^{0.78}$ $r^2 = 0.89$

Concerning back calculation, we applied the following formulae:

- before draining: $L_i = TL*Ri^{0.94}/TR^{0.94})$
- after refilling: $L_i = TL*(Ri^{0.78}/TR^{0.78})$

where L_i was the total length corresponding to the annulus 'i' and R_i was the radius of annulus 'i'.

Back-calculated lengths and the standard growths (i.e. mean annual increments) for the two periods studied are represented in *figures 3* and *4*. Considering each age studied (1^+, 3^+ and 4^+ roach), significant differences in back-calculated lengths were found between the two sampling periods (Mann-Whitney test: the length at 1 year for 1^+ roach $U = 546$ $p < 0.001$; at 1 year for 3^+ roach $U = 10$, at 2 years $U = 8$, at 3 years $U = 16$: $p < 0.001$; at 1 year for 4^+ roach $U = 83$, at 2 years $U = 0$, at 3 years $U = 2$, at 4 years $U = 5$: $p < 0.001$). A comparison of paired values of annual length increments by the Mann-Whitney test (at 1 year for 3^+ roach $U = 10$ $p < 0.001$, at 2 years $U = 107$ $p < 0.01$; at 1 year for 4^+ roach $U = 7$ $p < 0.001$, at 2 years $U = 353$ $p < 0.001$) showed that the first 2 years of growth of 3^+ and 4^+ were responsible for the heterogeneity between the two sampling periods. Thus, the difference in roach size observed before and after draining was mainly due to the greater fish growth during the first 2 years of their life.

4. Discussion

Population length and age structure showed that roach grew faster after refilling. The back-calculated lengths after draining were high compared to available published results (*table II*). Moreover, the growth rate before draining was close to values obtained for stunted roach populations in two English lakes (*table II*). Fish growth is dependent on water temperature [20, 27, 28] but in this study, the temperature hardly differed between the two periods (*table I*), so roach growth comparisons were not biased.

The difference in standard growth rates before and after refilling during the first 2 years of growth could be due to the lower fish biomass observed after refilling. Fish reintroduced after refilling (i.e. 1994) accounted for less than 20 $kg{\cdot}ha^{-1}$ [29], whereas their biomass had been estimated at 68 $kg{\cdot}ha^{-1}$ before draining [30]. Four years after refilling, roach density was 13 % lower than that recorded before draining. The growth rate of a fish population is closely linked to the density of individuals and food availability [5, 6, 31]. More precisely, Carlander [4] considered that the population density, related to the carrying capacity of the habitat, was the major environmental factor controlling the growth of individual fish. Fewer roach in the lake leads to a diminution of intraspecific feeding competition [22] and thus, increased growth.

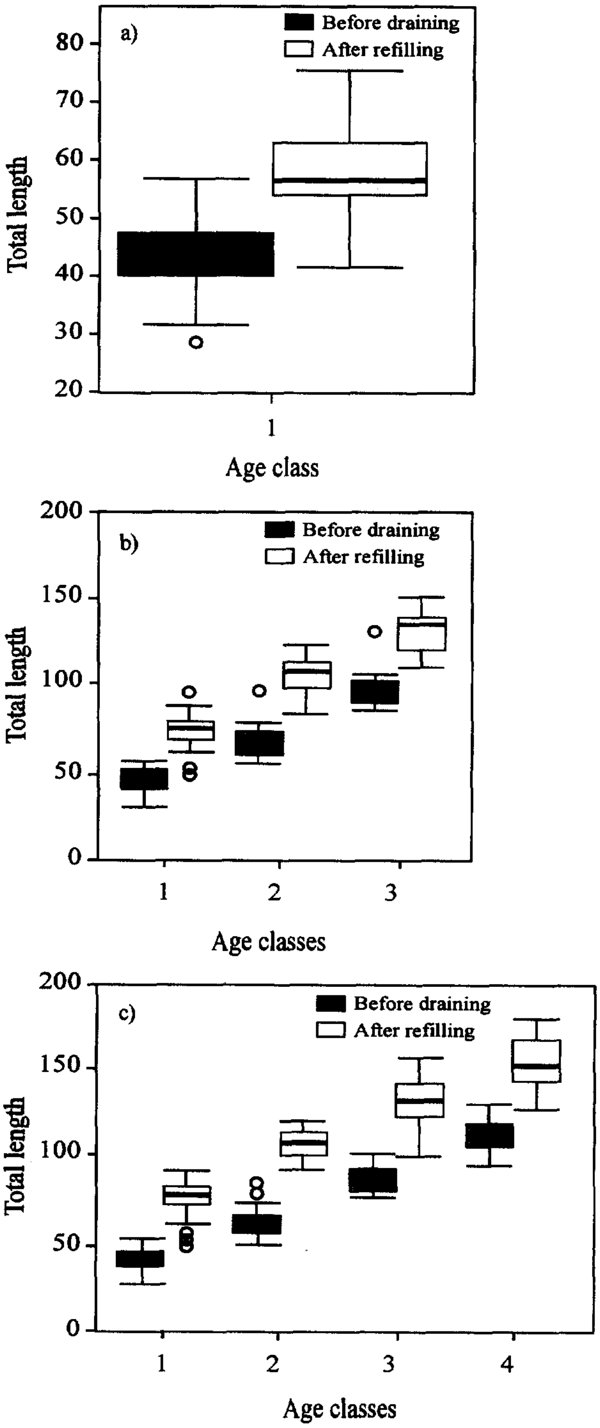

Figure 3. Boxplots of backcalculated roach total lengths.
The top, mid-line and bottom of each box represent the 75th, 50th and 25th percentiles, respectively; the horizontal lines represent the 10th and 90th percentiles; open circles represent units in which values were more than 1.5 box-lengths from the 75th percentile (outliers). **a:** Back-calculated length of 1^+ roach before and after draining; **b:** back-calculated length of 3^+ roach before and after draining; **c:** back-calculated length of 4^+ roach before and after draining.

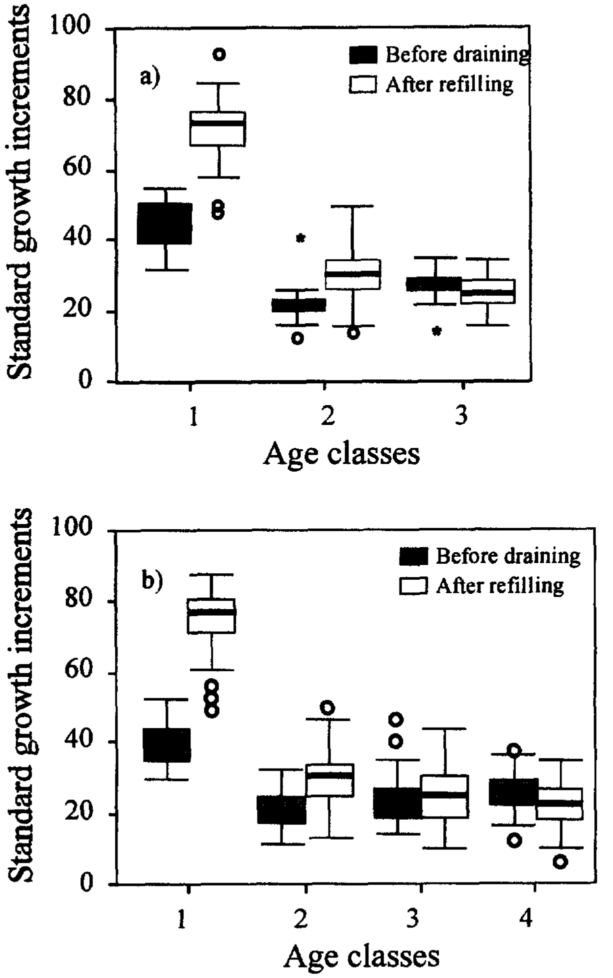

Figure 4. Boxplot of standard growth increments calculated from backcalculated lengths.
The top, mid-line and bottom of each box represent the 75th, 50th and 25th percentiles, respectively; the horizontal lines represent the 10th and 90th percentiles; open circles represent units in which values were more than 1.5 box-lengths from the 75th percentile (outliers); asterisks represent units in which values were more than 3 box-lengths from the 75th percentile (extremes). **a**: Standard growth increments of 3^+ roach before and after draining; **b**: standard growth increments of 4^+ roach before and after draining.

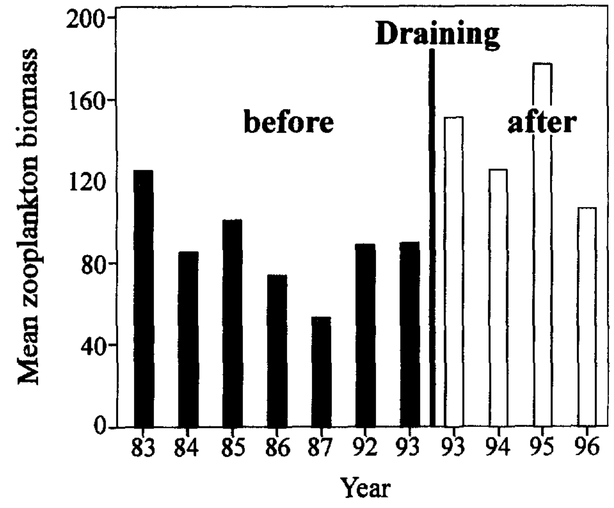

Figure 5. Zooplankton mean annual biomass expressed in μg dry weight before and after draining. (Francisco, unpubl. data.)

Roach are known to use almost any kind of food source [5, 32]. They feed on a wide spectrum of food items such as detritus, phytoplankton, zooplankton and macroinvertebrates [21, 33]. Studies of their diet showed that zooplankton is the main food item during the first 2 years of growth. Ingestion of detritus and algae never exceeds 13 % of the diet for the young of the year, whereas it increases for the older fish [34, 35]. In lake Pareloup, after refilling, the mean annual zooplankton biomass increased, reaching 154 μg dry weight after refilling (*figure 5*). Zooplankton densities found in 1993, 1994 and 1995 were always greater than those found before draining (*figure 5*). Moreover, a significant increase in the lipid and protein content of zooplankton was observed after refilling [29]. This higher quality and quantity of zooplankton must have contributed to improved roach growth after refilling especially during the first 2 years of their life when zooplankton constituted their main food item.

Our results agree with those of Hartmann [36], which showed a roach density increase that paralleled the eutrophication level. Before draining, the eutrophication level was high and there was a larger number of roach than after refilling. Our results underline a rise in roach growth induced by the draining of the reservoir which can be assimilated to a rejuvenation of the aquatic ecosystem. Owing to their opportunistic habitat use and breeding behaviour [37, 38], roach can easily adjust to environmental changes, and consequently they can optimise their growth rate. Moreover, the disappearance of aquatic vegetation induced by the draining was unfavourable for perch [39, 40]. Thus, feeding competition on zooplankton due to 0^+ and 1^+ perch was reduced, allowing an increase in the growth rate of the roach during their first years of life.

Before draining, the lake Pareloup fish population appeared saturated. Owing to draining, it was no longer saturated and so more propitious to fish growth through reduced feeding competition and the higher dietary quality of the zooplankton. Thus, the improved quantity and quality of feeding resources allowed the 0^+ and 1^+ roach to grow faster after refilling in accordance with the Odum [41] overshoot theory. The present study underlines the importance of monitoring fish during their first 2 years of life when their growth potential is greatest to better understand aquatic ecosystem evolution.

The draining and refilling of a lake can be considered as beginning its ecological evolution anew. After refilling, lake Pareloup was in the trophic explosion phase as defined by Balvay [13]. This maturation stage, characteristic of the beginning of ecosystem maturation, tends to be favourable to fast growing animals such as young-of-the-year fish. Moreover, owing to their status in the higher lev-

Table II. Growth of several populations of roach *Rutilus rutilus* expressed in mm.

Site	Age (year)							Reference
	1	2	3	4	5	6	7	
Pareloup before draining, F (l)	41	63	87	111	133			
Pareloup after refilling, F (l)	72	102	129	153	167			
Aydat, F (l) *	60	90	115	136	155	170	183	[19]
Geneva, F (l) (e)	82	130	171	207	239	243	275	[20]
Sainte-Croix, F (l) (o)	60	116	157	191	213	231	244	[21]
Slapton Ley, GB (l) *	42	76	98	113	153			[22]
Grey Mist Mere, GB (l) *	46	93	101	106	109			[23]
Tjeukemeer, NL (l)	51	84	108	129	145			[24]
Malaren, S (l)	42	76	111	140	161			[7]
Sövdeborgssjön, S (l)	55	80	110	126	156			[25]
Pilica 1, P (r)	71	96	124	158	179	195	223	[26]
Pilica 2, P (r)	72	97	128	144	181	193	222	[26]

l = lake, r = river, o = oligotrophic, e = eutrophic, F = France, GB = Great Britain, NL = Netherlands, S = Sweden, P = Poland, * = stunted roach population.

els of the trophic chain, the fish are strongly affected by the variations of the lower stages of the chain, such as phytoplankton and zooplankton. Thus, young-of-the-year fish growth appears to constitute a precise and easily measurable indicator of the state of trophic evolution of lakes.

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