Arch. Hydrobiol. 149 2 271–284 Stuttgart, September 2000

Introduction of exotic fish into a Mediterranean lake over a 90-year period

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With 5 figures and 1 table

Abstract: The impact of exotic species is a neglected, worldwide ecological problem, particularly for freshwater fish. Examples of historical changes in southern Europe due to fish introduction are rare. Lake Banyoles, the second largest lake of the Iberian Peninsula, has suffered a long history of fish introductions. We reviewed the historical changes in the fish assemblage and assessed its current state in a field study. Before 1910, only five or six native species were present. During this century up to 12 exotic species were introduced, leading to the apparent loss of two native species (three-spined stickleback *Gasterosteus aculeatus* and, possibly introduced several centuries ago, tench *Tinca tinca*) and the decline of three others (eel *Anguilla anguilla,* chub *Leuciscus cephalus,* and barbel *Barbus meridionalis*). The current fish assemblage is dominated by exotic species, particularly the largemouth bass (*Micropterus salmoides*) and the pumpkinseed sunfish (*Lepomis gibbosus*) in the littoral zone and roach (*Rutilus rutilus*) in the pelagic zone. The only native species still common nowadays is the freshwater blenny (*Salaria* (= *Blennius*) *fluviatilis*).

Introduction

The impact of introduced species is a neglected, worldwide ecological problem, especially in freshwater systems (COURTENAY & ROBBINS 1989, MOYLE 1997). There is an impressive record of successful inland fish invasions that have contributed to the loss of native species (TAYLOR et al. 1984, DI CASTRI 1991, COURTENAY 1993, LEVER 1996). Freshwater fish faunas are highly differentiated and isolated, particularly compared to marine fish. For this reason, the introduction of freshwater fish, which is common worldwide mainly for aquaculture and angling-related purposes, is especially harmful in terms of biodiversity.

Several authors (CRIVELLI 1995, ELVIRA 1995 a, KEITH & ALLARDI 1998) have pointed out that evidence of changes due to fish introductions is limited in southern Europe, mostly because few data on fish abundance are available.

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0003-9136/00/0149-0271 $ 3.50

In this paper we intend to fill this gap. We reviewed the historical changes in the fish assemblage of Lake Banyoles, the second largest lake of the Iberian Peninsula. We also assessed its current state through a field study. Due to the scarcity of lakes in the Iberian Peninsula, Lake Banyoles has concentrated the attention of limnologists but has also suffered from pioneering attempts of fish introduction. As is the rule with exotic species (TAYLOR et al. 1984, MOYLE et al. 1986, ROSS 1991, COURTENAY 1993), their ecological impact is difficult to ascertain because precise data before the introduction are lacking. However, a number of points make the history of Banyoles invaluable: 1) fish records are available over a long period of time, 2) most introductions occurred long ago so the populations had some time to interact and evolve (BROWN & MOYLE 1997), and 3) no other disturbance is present, namely there are no commercial fisheries nor evidence of pollution or eutrophication because most water enters through underground sources.

Methods

Study area

Lake Banyoles, situated at 42° 7′ N, 2° 45′ E and 172 m above sea level in Catalonia (northeastern Spain), is of mixed tectonic–karstic origin. The mainly subterranean water sources and high calcium concentration restrict its productivity. Although usually considered oligotrophic because of the low nutrient concentration and phytoplankton biomass, it is rather mesotrophic based on its primary production and its benthic community. A number of studies are available on its morphometry (MORENO-AMICH & GARCÍA-BERTHOU 1989), hydrology (CASAMITJANA & ROGET 1993), bacterioplankton (GARCIA-GIL et al. 1996), phytoplankton (PLANAS 1973), zooplankton (MIRACLE 1976), and non-littoral zoobenthos (PRAT & RIERADEVALL 1995). Selected features of the lake are: surface area, 111.8 ha; mean depth, 14.8 m; water temperature, 7–26 °C; and conductivity, 0.9–2 mS cm^{-1}.

Literature survey

We surveyed the historical fish records from Lake Banyoles. The literature consisted of fish culture experiments early in the present century (DARDER 1913), bulletins of angling associations (Anonymous 1960–1965, Anonymous 1968), reports from the fisheries management agency (NADAL 1952, 1964, 1983), and a few other records (ELVIRA 1984, NADAL 1984, DOADRIO & ELVIRA 1985, SOSTOA et al. 1987, DOADRIO et al. 1988). Taxonomic clarification on the records and historical details are given in GARCÍA-BERTHOU (1994). The literature does not include precise abundance data but qualitative comments, so we classified the fish species in three abundance categories (abundant, common and rare).

The historical changes of the fish assemblage were summarised using the Jaccard index of similarity (see e.g., MAGURRAN 1988) referring to the unaltered assemblage, i.e., before 1910. The Jaccard index (C_J) for a certain historical period was calculated as $C_J = j/(a + b - j)$, where a = number of species present before 1910 (i.e., 6), b = number of species present in the historical period, and j = number of species present in both periods. This index ranges from 1 for identical samples (i.e., the unaltered assemblage) to 0 for completely different samples (i.e., if all the native species had disappeared).

Field study

Fish from Lake Banyoles were sampled quarterly from February 1990 to November 1991. Sampling was by boat electrofishing in the littoral and with trammel nets elsewhere (stretched mesh size: inner net, 2 cm; outer, 12.5 cm). Trammel nets are less size selective than gillnets so a broader range of fish sizes is obtained (HUBERT 1983). Electrofishing was ineffective and not used in summer. Pelagic trammel nets were placed at 5, 10, and 15 m depth and bottom trammel nets at 10 and 20 m (or 15 m for shallower basins). Nets were set for 24 h on six consecutive days. Dipnets were also used in two littoral sites. All captured fish (over 1,321 individuals) were immediately stored on ice and later frozen. In the laboratory, fish were measured (to the nearest 1 mm, except for mosquitofish and young-of-the-year to the nearest 0.1 mm) and used for dietary studies (GARCÍA-BERTHOU 1994, 1999 a, 1999 b).

Correspondence analysis (CA) was used on the number of fish captured by species and sample to describe the main sources of variation. CA is an ordination technique that reduces a species × sample matrix to a few dimensions explaining most of the variation. For community ecology data, CA generally performs better than principal component analysis (TER BRAAK 1987). All statistical analyses were performed with SPSS 6.0 for Windows.

Results

Historical changes in the fish assemblage

There are numerous fish records in the literature (Table 1) because Lake Banyoles is the second largest lake of the Iberian Peninsula and during this century has attracted the attention of limnologists and anglers. The fish assemblage before 1910 consisted of tench (possibly introduced several centuries ago, see Discussion), chub, Mediterranean barbel, eel, three-spined stickleback, and freshwater blenny.

Up to 12 fish species have been introduced into the lake during this century, paralleling the decline of the six native species (Table 1, Fig. 1). Other fish species might have been introduced after fish exhibitions early in this century (DARDER 1913). Three-spined stickleback and tench seem to have disappeared around 1960 and appear to be not present any longer in the lake. The eel and the barbel are now very rare. Because there is no other disturbance present in the lake, namely there are no commercial fisheries nor evidence of pollution or eutrophication, the decline of the native species seems to be

Table 1. Fish records in Lake Banyoles. Species are ordered by first record date. The dates with question marks seem speculative. Only the first five species are clearly native to the lake. References (given as superscripts): *a* = DARDER (1913), *b* = GIBERT (1912 a), *c* = GIBERT (1912 b), *d* = VIDAL (1925), *e* = NADAL (1952), *f* = COROMINAS (1960), *g* = Anonymous (1960–65), *h* = NADAL (1964), *i* = Anonymous (1968), *j* = NADAL (1983), *k* = ELVIRA (1984), *l* = DOADRIO & ELVIRA (1985), *m* = SOSTOA et al. (1987), *n* = DOADRIO et al. (1988), and *o* = this study.

Fish species		Family	Record date and reference
Common name	Scientific name		
Eel	*Anguilla anguilla* (L.)	Anguillidae	before 1910[e,h,j], 1910–1913[a], 1925[d], 1952[e], 1964[h], 1990–1991[o]
Barbel	*Barbus meridionalis* (RISSO)	Cyprinidae	before 1910[e,h,j], 1925[d], 1952[e], 1964[h], no date[n], 1991[o]
Freshwater blenny	*Salaria fluviatilis* (ASSO) (= *Blennius fluviatilis*)	Blenniidae	before 1910[j], 1964[h], 1990–1991[o]
Three-spined stickleback	*Gasterosteus aculeatus* L.	Gasterosteidae	before 1910[e,h,j], 1912[j], 1949–1950[e], 1964[h], 1983?[j]
Chub	*Leuciscus cephalus* (L.)	Cyprinidae	before 1910[h,j], 1925[d], 1952[e], 1964[h], 1990–1991[o]
Tench	*Tinca tinca* (L.)	Cyprinidae	before 1910[e,h,j], 1912[c], 1925[d], [j]1952[e], 1964[h]
Common carp	*Cyprinus carpio* L.	Cyprinidae	1910–1913[a,c,e,f,h,j], 1925[d], 1952[e], 1964[h] 1983[j], 1990–1991[o]
Black bullhead	*Ameiurus melas* (RAF.) (= *Ictalurus melas*)	Ictaluridae	1910–1913[f,h,j], 1950[k], 1983?[j]
Pumpkinseed sunfish	*Lepomis gibbosus* (L.)	Centrarchidae	1910–1913[f,h,j], 1952[e], 1964[m], 1980[m], 1983[j], 1990–1991[o]
Rainbow trout	*Oncorhynchus mykiss* (WALBAUM)	Salmonidae	1910–1913[a,e,j]
Brown trout	*Salmo trutta* L.	Salmonidae	1910–1913[a,e,j]
Rudd	*Scardinius erythrophthalmus* (L.)	Cyprinidae	1910–1913[e,f,h,j], 1925[d], 1952[e], 1964[h], 1983[j], 1990–1991[o]
Pike	*Esox lucius* L.	Esocidae	1954[j], 1960–1965[g], 1964[h], 1968[i], 1983?[j]
Goldfish	*Carassius auratus* (L.)	Cyprinidae	1964[h], no date[l]
Mosquitofish	*Gambusia holbrooki* GIRARD	Poeciliidae	1964[h], 1990–1991[o]
Largemouth bass	*Micropterus salmoides* (LACÉPÈDE)	Centrarchidae	1965–1967[j], 1983[j], 1990–1991[o]
Roach	*Rutilus rutilus* (L.)	Cyprinidae	1990–1991[o]
Perch	*Perca fluviatilis* L.	Percidae	1991[o]

clearly due to the introduction of the exotic species (see also MOYLE & LIGHT 1996 a).

Some of the introduced species, namely the salmonids (including the brown trout and the rainbow trout) and the black bullhead, did not succeed to colonise the lake. However, they colonised the main river basin (Ter River), where some of them are present nowadays.

The Jaccard index (Fig. 2) summarises the changes in the fish assemblage. There are two steep decreases in similarity, in the 1910s and 1950s, when most introductions were carried out. These are followed by two longer periods without changes in the presence of species. The final value indicates a 33 % of similarity between the present assemblage and the original one. An index considering the abundance of species would be even lower.

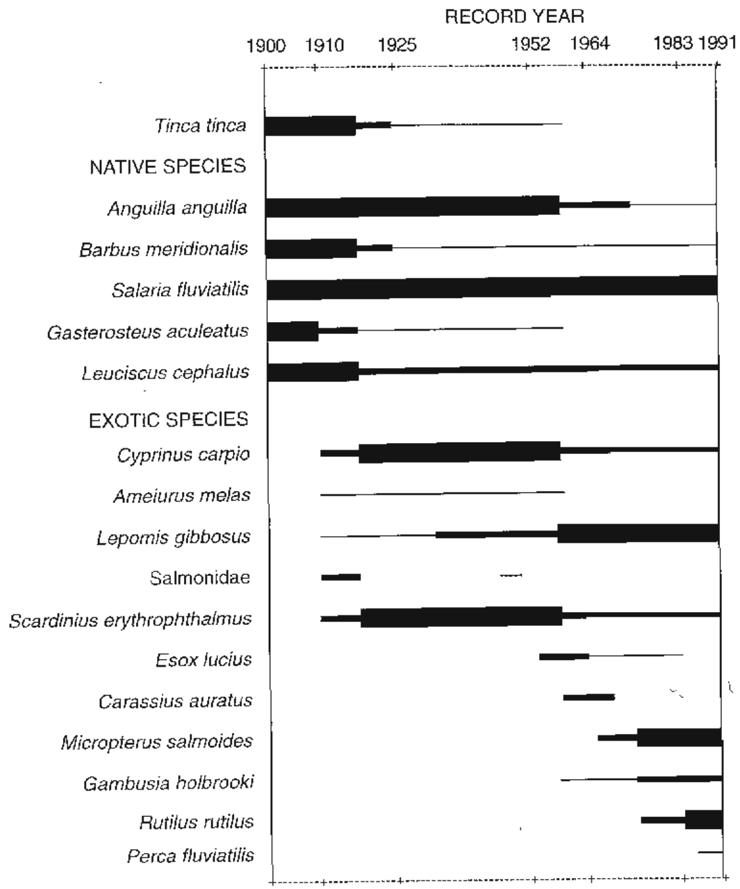

Fig. 1. Population dynamics of the fish assemblage of Lake Banyoles according to the literature comments and its present state. The thickness of the lines is proportional to the species abundance, classified as abundant, common or rare.

Fish abundance and habitat partitioning

The lake is nowadays dominated by exotic species. The most common fish species are the largemouth bass and the pumpkinseed sunfish in the littoral and roach in the pelagic zone (see catch numbers in Fig. 3 and 5). The only native species still common nowadays is the freshwater blenny. Although the freshwater blenny was not well captured with our sampling gears, other data (GARCÍA-BERTHOU, personal observation; see also VILA-GISPERT & MORENO-

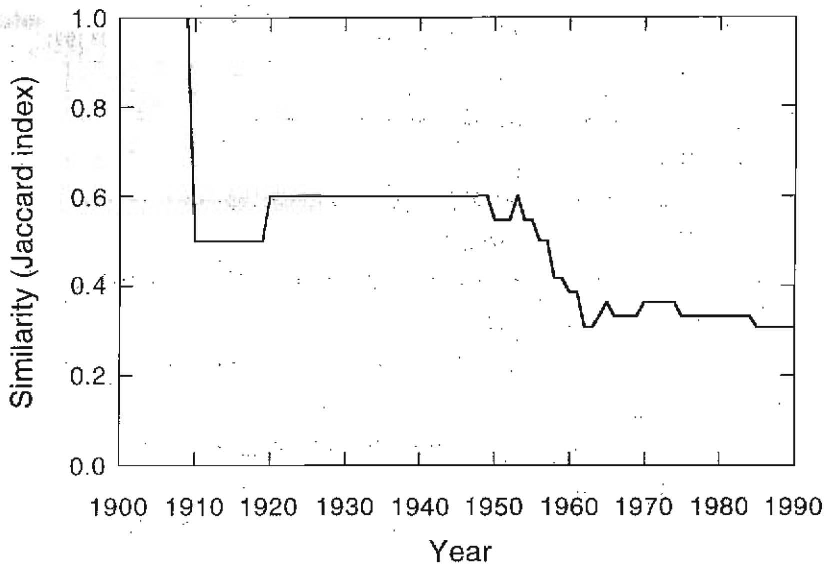

Fig. 2. Historical changes in similarity (Jaccard index) of the fish assemblage of Lake Banyoles referred to its original state (before 1910).

Amich 1998) show that it is common. The size structure (Fig. 3) is dominated by large fish, particularly for carp, chub, and eel, which lack young individuals because of recruitment problems.

A correspondence analysis (CA) of the number of fish captured shows a clear pattern of habitat partitioning (Fig. 4). The first two dimensions jointly explained 35.1 % of the variation. The first dimension distinguishes the smallest fish species (mosquitofish and freshwater blenny) inhabiting the more vegetated, shallowest areas of the littoral. The second dimension was significantly related to sample depth ($r = -0.77$, $n = 239$, $P < 0.00005$) and separated the littoral species (largemouth bass, pumpkinseed sunfish, and rudd) from the more pelagic species. The depth variation in fish abundance is shown in Fig. 5, confirming this interpretation.

Discussion

Historical changes

Two distinct historical periods are apparent in the change of the fish assemblage. During the first half of the century the fish community was dominated by cyprinid species, particularly rudd and common carp, which were stunted (Vidal 1925). These two exotic cyprinids are typical of eutrophic lakes, so they should not be expected to adapt well to an oligotrophic lake. However, they

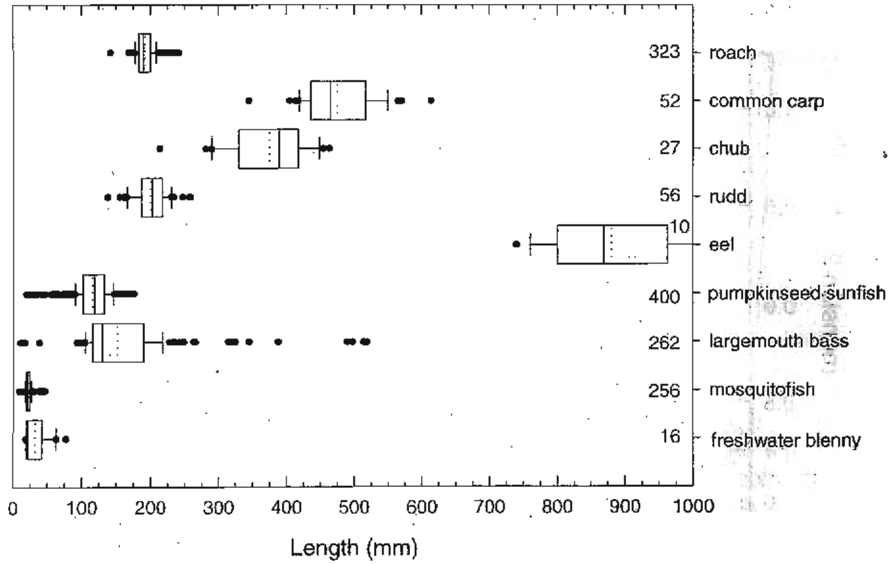

Fig. 3. Size structure of the fish assemblage of Lake Banyoles in 1990–1991. Box plot of fork length (total length for eel, blenny, and mosquitofish) are shown for each fish species. The box corresponds to the 25th and 75th percentiles, the continuous line inside the box represents the median length (50 %), the dotted line is the mean, error bars are the 10th and 90th percentiles, and the dots are the remaining data (outliers). The figures (beside the species name) are the numbers of fish captured. The rarest fish (3 barbel and 2 perch) are not included.

apparently had two clear effects in Lake Banyoles during this period: a decline of submerged macrophytes (Vidal 1925); and the near disappearance of native cyprinids (barbel and chub) and the three-spined stickleback through competition, egg predation, and the loss of habitat (plant beds). The decline of macrophytes is common with the introduction of cyprinids. Rudd are among the most herbivorous European cyprinids and are the most herbivorous fish in the current assemblage of the lake (García-Berthou 1994). Common carp reduce the abundance of macrophytes by direct consumption and by uprooting associated to their feeding behaviour (Crivelli 1983, Taylor et al. 1984).

The second half of the century is characterised by the introduction of two notable piscivores, the pike and the largemouth bass. These were expected to control the cyprinids and improve angling. The introduction of these top predators apparently accelerated the extinction and decline of native species and has also resulted in a size structure of populations dominated by large individuals (Fig. 3). Catastrophic impacts due to the introduction of piscivorous fish are well documented (Taylor et al. 1984, Fernando 1991, Poe et al. 1994, Moyle & Light 1996 a); the most dramatic case being the extinction of more than 100 species of endemic cichlids in Lake Victoria due to the introduction of

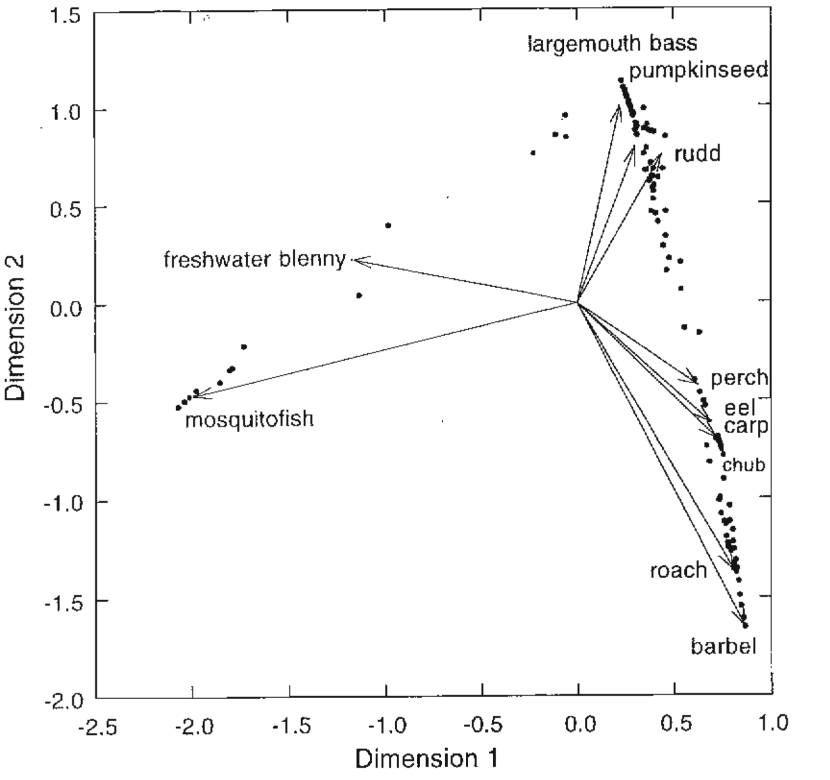

Fig. 4. Correspondence analysis of the number of fish captured by species and sample in Lake Banyoles during 1990–1991. The sample and species factor scores for the first two dimensions are shown.

the Nile perch (*Lates niloticus*) (KAUFMAN 1992, LÉVÊQUE 1998). Similar ecological impacts of the pike and the largemouth bass throughout the world are reviewed by LEVER (1996).

Biological invasions and assembly theory

The history of Lake Banyoles overall agrees with the empirical rules on biological invasions proposed by MOYLE & LIGHT (1996 a, 1996 b). Thus, in addition to the frequent impact of piscivores, the strong effects observed in the lake correspond to a system with low variability and severity and with low native species richness. The exceptions are that most exotic species succeeded to become established in the lake (7 out of 12) and that despite the low human alteration of the lake the long-term success of many of the exotic species seems likely.

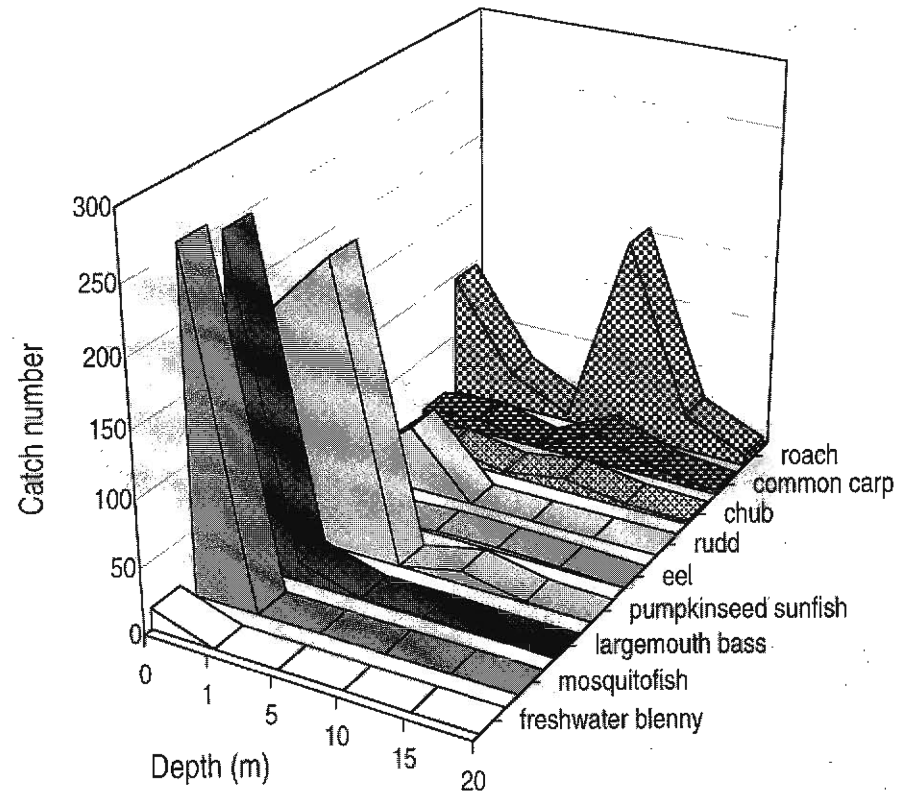

Fig. 5. Depth variation in number of individuals captured by fish species. The rarest fish (barbel and perch) are not included.

The current fish assemblage displays clear ecological segregation in habitat (see Results) and food resources (GARCÍA-BERTHOU 1994). This pattern agrees with a system with low environmental variability and severity, in which biotic factors are more important.

Conservation implications

The freshwater populations of the three-spined stickleback are threatened in contrast to its brackishwater populations (LELEK 1987). The loss of the population in Banyoles is unfortunate because it was probably one of the most important freshwater populations in the Iberian Peninsula, where both lakes and stickleback are rare (DOADRIO et al. 1991).

The freshwater blenny is the only native species still common in the lake, despite the presence of exotic top predators. This conservation is fortunate and should be ensured because this species is among the few Spanish fish considered to be "endangered" (ELVIRA 1995 b). Of the 51 Spanish native inland fish listed by BLANCO & GONZÁLEZ (1992), only 6 are endangered and 1 is apparently extinct. The persistence of the blenny seems to be related to its particular ecological features, namely its cryptic morphology, small size, and benthic, littoral habitat.

The eel decline is not related to fish introduction. The eel population of Banyoles is constituted by a few old individuals. The decline of this species is due to the high level of pollution of the lake outflow (Terri river), which prevents migration. The ongoing restoration of the Terri River should allow reproductive migration of adult eels and arrival of juveniles.

Management suggestions

The effects of exotic freshwater fish are a worldwide neglected ecological problem. Clearly, in most cases there is not enough information to justify a harmless introduction. In Lake Banyoles and the Iberian Peninsula in general, new exotic species continue to be introduced, with no concern on the part of anglers, the general public, or the government. The main mechanism of introduction and dispersal is via anglers. Obviously, many of these introductions are irreversible because restoration seems to be virtually impossible (see e.g., BALTZ & MOYLE 1993). We urge the Spanish government to take this problem into consideration. Following are two specific points directly derived from our results.

It is unclear whether the tench is native to Lake Banyoles and the Iberian Peninsula in general or whether it was introduced several centuries ago. It is difficult to accurately separate the original distribution of the tench from that resulting from fish culture and stocking (LOBÓN-CERVIÁ et al. 1989, DOADRIO et al. 1991). For instance, GIBERT (1912 b) points out that tench in ponds from Lleida (another Catalan province) were probably introduced by monks before 1735. ALMAÇA (1995) also reports the introduction of tench to a Portuguese river by monks during the Middle Ages in order to be used as food in days on which the consumption of meat was not allowed. Monks also managed Lake Banyoles and its fisheries from the ninth to the seventeenth centuries (RIGAU 1990) and thus the introduction of tench seems likely. Similarly, BIANCO (1998) suggested that tench were probably introduced to Italy during the Roman period or Middle Ages. Therefore, we suggest to avoid the stocking of tench in the Iberian Peninsula until this question has been clarified. Tench might correspond to what CARLTON (1996) termed a "cryptogenic species", i.e. a species that is not demonstrably native or introduced. Historical and archaeological data might give some insight into this question, as was the case with the common carp (BALON 1995).

Lake Banyoles was the very first site in the Iberian peninsula where some of these species (rudd, black bullhead, and pumpkinseed sunfish) were introduced. The eastern Pyrenees are the Spanish region with the second most exotic fish species (ELVIRA 1995 a). Some exotic fish species (e.g., rudd, black bullhead, roach, and perch) are almost only present in Catalonia (DOADRIO et al. 1991), and the Ter river (the watershed of Lake Banyoles) is one of the Iberian rivers with the highest number of exotic species (14 out of the 20 introduced to Spain). We believe that this high presence of exotics is due to a combination of factors: the singularity of Lake Banyoles, which has attracted the attention of limnologists and anglers among others; the proximity of the Pyrenees mountains, a strong biogeographical barrier that constitutes the southern limit of many European species not native to the Iberian Peninsula (e.g., pike, roach, perch, and rudd); and the geographical situation of Catalonia, including part of the lowest Pyrenees, as the natural entrance to the Peninsula. We suggest that preventing the introduction of exotic fish into Catalonia is a key measure for controlling their spread into the Iberian Peninsula.

Acknowledgements

We would like to thank everybody who assisted in field and laboratory work, especially QUIM PAREDES and DANI BOIX. This study was financially supported by the Town Council of Banyoles (grant to RMA) and the Autonomous Government of Catalonia (FI fellowship and CIRIT grant AR89 to EGB). CARLOS GRANADO-LORENCIO and JOSÉ PRENDA provided helpful advice on the sampling methods. The manuscript greatly benefited from insightful comments by BENIGNO ELVIRA, N. C. MORGAN, an anonymous reviewer, and particularly PETER B. MOYLE.

References

ALMAÇA, C. (1995): Fish species and varieties introduced into Portuguese inland waters. – Museu Nacional de História Natural, Lisboa.

Anonymous (1960–1965): Boletín Asociación de Pescadores Deportivos 'El Lago' **4–29.**

– (1968): Boletín Sociedad de Pesca Deportiva 'La Caña'.

BALON, E. K. (1995): Origin and domestication of the wild carp, *Cyprinus carpio*: from Roman gourmets to the swimming flowers. – Aquaculture **129:** 3–48.

BALTZ, D. M. & MOYLE, P. B. (1993): Invasion resistance to introduced species by a native assemblage of California stream fishes. – Ecol. Appl. **3:** 246–255.

BIANCO, P. G. (1998): Freshwater fish transfers in Italy: history, local changes in fish fauna and a prediction on the future of native populations. – In: COWX, I. G. (ed.): Stocking and introduction of fish. – Fishing News Books, Oxford, pp. 167–185.

BLANCO, J. C. & GONZÁLEZ, J. L. (eds.) (1992): Libro rojo de los vertebrados de España. – ICONA, Madrid.

Brown, L. R. & Moyle, P. B. (1997): Invading species in the Eel River, California: successes, failures, and relationships with resident species. – Envir. Biol. Fish. **49:** 271–291.

Carlton, J. T. (1996): Biological invasions and cryptogenic species. – Ecology **77:** 1653–1655.

Casamitjana, X. & Roget, E. (1993): Resuspension of sediment by focused groundwater in Lake Banyoles. – Limnol. Oceanogr. **38:** 643–656.

Corominas, J. M. (1960): Darder en Bañolas. – Boletín Asociación de Pescadores Deportivos 'El Lago' **5**.

Courtenay, W. R. Jr. (1993): Biological pollution through fish introductions. – In: McKnight, B. N. (ed.): Biological pollution: the control and impact of invasive exotic species. – Indiana Academy of Science, Indianapolis, pp. 35–61.

Courtenay, W. R. Jr. & Robins, C. R. (1989): Fish introductions: good management, mismanagement, or no management? – CRC Critical Reviews in Aquatic Sciences **1:** 159–172.

Crivelli, A. J. (1983): The destruction of aquatic vegetation by carp. – Hydrobiologia **106:** 37–41.

– (1995): Are fish introductions a threat to endemic freshwater fishes in the northern Mediterranean region? – Biol. Conserv. **72:** 311–319.

Darder, F. (1913): Piscicultura. Cronica piscatoria. – Publicaciones del Aquarium de Barcelona, Barcelona.

di Castri, F. (1991): The biogeography of Mediterranean animal invasions. – In: Groves, R. H. & di Castri, F. (eds.): Biogeography of Mediterranean invasions. – Cambridge Univ. Press, Cambridge, pp. 439–452.

Doadrio, I. & Elvira, B. (1985): Distribución geográfica actual del género *Carassius* Jarocki, 1822 (Ostariophysi, Cyprinidae) en España. – Miscellània Zoològica **10:** 385–387.

Doadrio, I., Elvira, B. & Bernat, Y. (eds.) (1991): Peces continentales españoles. Inventario y clasificación de zonas fluviales. – ICONA, Madrid.

Doadrio, I., de Sostoa, A., Fernández, J. V. & de Sostoa, F. J. (1988): Sobre la distribución de *Barbus meridionalis* Risso 1826 (Ostariophysi, Cyprinidae) en la Península Ibérica. – Doñana, Acta Vertebrata **15:** 151–153.

Elvira, B. (1984): First records of the North American catfish *Ictalurus melas* (Rafinesque, 1820) (Pisces, Ictaluridae) in Spanish waters. – Cybium **8:** 96–98.

– (1995 a): Native and exotic freshwater fishes in Spanish river basins. – Freshwat. Biol. **33:** 103–108.

– (1995 b): Conservation status of endemic freshwater fish in Spain. – Biol. Conserv. **72:** 129–136.

Fernando, C. H. (1991): Impacts of fish introductions in tropical Asia and America. – Can. J. Fish. Aquat. Sci. **48:** 24–32.

García-Berthou, E. (1994): Ecologia alimentària de la comunitat de peixos de l'Estany de Banyoles. – Ph.D. dissertation, Univ. of Girona, Girona, Spain.

– (1999 a): Spatial heterogeneity in roach (*Rutilus rutilus*) diet among contrasting basins within a lake. – Arch. Hydrobiol. **146:** 239–256.

– (1999 b): Food of introduced mosquitofish: ontogenetic diet shift and prey selection. – J. Fish Biol. **55:** 135–147.

García-Berthou, E. & Moreno-Amich, R. (2000): Food of introduced pumpkinseed sunfish: ontogenetic diet shift and seasonal variation. – J. Fish Biol. **57:** 29–40.

Garcia-Gil, L. J., Casamitjana, X. & Abella, C. A. (1996): Comparative study of two meromictic basins of Lake Banyoles (Spain) with sulphur phototrophic bacteria. – Hydrobiologia **319:** 203–211.

Gibert, A. M. (1912 a): Fauna ictiológica de Catalunya. Catálech rahonat dels peixos observats en el litoral y en les aygues dolses catalanes. – Butll. Inst. Cat. Hist. Nat. **10:** 138–157.

– (1912 b): Fauna ictiológica de Catalunya, Catálech rahonat dels peixos observats en el litoral y en les aygues dolses catalanes. – Butll. Inst. Cat. Hist. Nat. **9:** 170–188.

Hubert, W. A. (1983): Passive capture techniques. – In: Nielsen, L. A. & Johnson, D. L. (eds.): Fisheries techniques. – American Fisheries Society, Bethesda MD, pp. 95–122.

Kaufman, L. (1992): Catastrophic change in species-rich freshwater ecosystems. – BioScience **42:** 846–858.

Keith, P. & Allardi, J. (1998): The introduced freshwater fish of France: status, impacts and management. – In: Cowx, I. G. (ed.): Stocking and introduction of fish. – Fishing News Books, Oxford, pp. 153–166.

Lelek, A. (1987): The freshwater fishes of Europe. Vol. 9. Threatened fishes of Europe. – AULA-Verlag, Wiesbaden.

Lévêque, C. (1998): Fish species introductions in African fresh waters. – In: Cowx, I. G. (ed.): Stocking and introduction of fish. – Fishing News Books, Oxford, pp. 234–257.

Lever, C. (1996): Naturalized fishes of the world. – Academic Press, London.

Lobón-Cervía, J., Elvira, B. & Rincón, P. A. (1989): Historical changes in the fish fauna of the River Duero basin. – In: Petts, G. E. (ed.): Historical Changes of Large Alluvial Rivers: Western Europe. – Wiley, Chichester, pp. 221–232.

Magurran, A. E. (1988): Ecological diversity and its measurement. – Croom Helm, London.

Miracle, M. R. (1976): Distribución en el espacio y en el tiempo de las especies del zooplancton del lago de Banyoles. – Monografías ICONA **5:** 1–270.

Moreno-Amich, R. & García-Berthou, E. (1989): A new bathymetric map based on echo-sounding and morphometrical characterization of the Lake of Banyoles (NE-Spain). – Hydrobiologia **185:** 83–90.

Moyle, P. B. (1997): The importance of a historical perspective: fish introductions. – Fisheries **22:** 14.

Moyle, P. B., Li, H. W. & Barton, B. A. (1986): The Frankenstein effect: impact of introduced fishes on native fishes in North America. – In: Stroud, R. H. (ed.): Fish Culture in Fisheries Management. – American Fisheries Society, Bethesda MD, pp. 415–426.

Moyle, P. B. & Light, T. (1996 a): Biological invasions of fresh water: empirical rules and assembly theory. – Biol. Conserv. **78:** 149–161.

– – (1996 b): Fish invasions in California: do abiotic factors determine success? – Ecology **77:** 1666–1670.

Nadal, J. (1952): Ríos y lagos de Gerona. Guía de pesca deportiva en sus aguas dulces. – Publicaciones de la Federación Española de Pesca **9:** 1–37.

NADAL, J. (1964): La pesca fluvial en Gerona. – Ed. del G.E.i.E.G. **1:** 1–59.
– (1983): Els peixos i la pesca a l'Estany de Banyoles. – Unpublished report of the Spanish Fisheries Federation.
– (1984): Els nostres peixos. – Diputació de Girona, Girona.
PLANAS, M. D. (1973): Composición, ciclo y productividad del fitoplancton del lago de Banyoles. – Oecologia aquatica **1:** 1–106.
POE, T. P., SHIVELY, R. S. & TABOR, R. A. (1994): Ecological consequences of introduced piscivorous fishes in the lower Columbia and Snake rivers. – In: STOUDER, D. J., FRESH, K. L. & FELLER, R. J. (eds.): Theory and application of fish feeding ecology. – University of South Carolina Press, Columbia SC, pp. 347–360.
PRAT, N. & RIERADEVALL, M. (1995): Life cycle and production of Chironomidae (Diptera) from Lake Banyoles (NE Spain). – Freshwat. Biol. **33:** 511–524.
RIGAU, A. M. (1990): Una volta a l'Estany de Banyoles. – Edicions de Nou Art Thor, Barcelona.
ROSS, S. T. (1991): Environmental structuring stream fish assemblages: are there lessons from introduced species? – Envir. Biol. Fish. **30:** 359–368.
SOSTOA, A. DE, LOBÓN-CERVIÁ, J., FERNÁNDEZ-COLOMÉ, V. & SOSTOA, F. J. DE (1987): La distribución del pez-sol (*Lepomis gibbosus* L.) en la Península Ibérica. – Doñana, Acta Vertebrata **14:** 121–123.
TAYLOR, J. N., COURTENAY, W. R. Jr. & MCCANN, J. A. (1984): Known impacts of exotic fishes in the continental United States. – In: COURTENAY, W. R. Jr. & STAUFFER, J. R. Jr. (eds.): Distribution, biology and management of exotic fishes. – John Hopkins Univ. Press, Baltimore MD, pp. 322–373.
TER BRAAK, C. J. F. (1987): Ordination. – In: JONGMAN, R. H. G., TER BRAAK, C. J. F. & VAN TONGEREN, O. F. R. (eds.): Data analysis in community and landscape ecology. – Pudoc, Wageningen, pp. 91–173.
VIDAL, J. (1925): L'estany de Banyoles. – Tipografía La Económica, Girona.
VILA-GISPERT, A. & MORENO-AMICH, R. (1998): Seasonal abundance and depth distribution of *Blennius fluviatilis* and introduced *Lepomis gibbosus*, in Lake Banyoles (Catalonia, Spain). – Hydrobiologia **386:** 95–101.

Submitted: 22 December 1999; accepted: 10 March 2000.