

Artificial macrophytes as fish habitat in a Mediterranean reservoir subjected to seasonal water level disturbances

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Abstract Artificial macrophytes were experimentally deployed in Boadella Reservoir (NE Spain) and assessed for fish use throughout the first 3 months of the 2007 summer drawdown. In total, 1,832 individuals of seven fish species were recorded through visual censuses, with introduced perch *Perca fluviatilis* being the prevalent species. Fish richness and abundance were significantly higher in artificial macrophytes than in rocky shores and sandy

beaches, displaying a unimodal variation through time. *P. fluviatilis*, *Rutilus rutilus* and *Abramis brama* were significantly more abundant in artificial macrophytes than in the other two naturally submersed habitats, where no individuals of these species were recorded. The abundances of *Squalius laietanus*, *Lepomis gibbosus*, *Micropterus salmoides* and *Cyprinus carpio* were overall greater in artificial macrophytes than in rocky shores but displayed significant habitat × time interactions. A decrease in predation risk was apparently the key-factor of the intensive use of artificial macrophytes by small fish (≤ 100 mm TL) in Boadella Reservoir, since most species reduced drastically or completely the use of submerged structures when body size increased. This study demonstrates that adding artificial structures mimicking aquatic macrophytes can be an interesting tool to mitigate the adverse effects of water level fluctuations on fish assemblages in structure-less and homogeneous ecosystems, and to understand the mechanisms affecting habitat use and species replacement.

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Introduction

River impoundment is one of the main anthropogenic causes of diversity loss in freshwater fishes (Dudgeon et al. 2006). Even if the impacts of reservoir filling are reduced with time, water level fluctuations, often due to dam operation, may continue to disrupt fish assemblages (Agostinho et al. 1999; Beklioglu et al. 2006). Rising water levels expand the littoral zone of reservoirs, and may increase shelter and food availability and improve fish condition and reproductive success (Sammons et al. 1999;

Sutela et al. 2002; Santos et al. 2004). Drawdowns often worsen fish condition, heighten biotic interactions, and may increase fish mortality, through impairment of water quality, destruction of littoral habitats, and exposition of eggs to desiccation (Piet 1998; Yamamoto et al. 2006; Benejam et al. 2008).

Although the impacts of water level fluctuations on reservoir fish have been relatively well documented, few prevention or mitigation practices to reduce them are available to managers. Although potentially useful, controlled water level manipulation for fish habitat improvement generally presents conflicts with reservoir uses such as hydroelectricity production and water abstraction (Summerfelt 1993; Miranda 1996; Agostinho et al. 2007). Seeding the reservoir withdrawal zones with grasses or replanting the fluctuating littoral areas with aquatic macrophytes is not successful for a number of reasons (Strange et al. 1982; Engel 1995; Strakosh et al. 2005; Smiley and Dibble 2006). Artificial structures have been experimentally deployed in reservoirs for a variety of purposes, such as to attract and concentrate fishery resources, enhance substrate for fish reproduction, increase shelter for juvenile or forage fish, and create new habitats in structure-less ecosystems (Nash et al. 1999; Bolding et al. 2004; Wills et al. 2004), but their potential to mitigate the drawdown impacts on fishes is little known (but see Benoît and Legault 2002; Santos et al. 2008).

In this paper, the role of artificial structures mimicking aquatic macrophytes as fish habitat in Boadella Reservoir, a 364 ha impoundment located in NE Spain, was investigated during a typical, severe summer drawdown. Boadella, like many others Mediterranean man-made lakes in Western Europe, is a structure-less and homogeneous reservoir that experiences remarkable seasonal water level fluctuations (Serra et al. 2002). The objectives of this work are: (1) to test whether fish abundance and richness increased in artificial macrophytes compared to naturally submerged habitats, by providing additional refuge for fish during reservoir dewatering; and (2) to compare colonisation patterns and habitat use by different fish species. The potential use of artificial macrophytes as a mitigative tool of drawdown disturbances on reservoir fish assemblages is also discussed.

Methods

Study area

Boadella Reservoir (42°20'15"N–2°21'07"E) is a 364 ha impoundment, located at 159 m a.s.l. in the Pyrenees slopes of Catalonia, NE Spain (Fig. 1). This reservoir was built in 1968 in the Muga River basin, mainly for

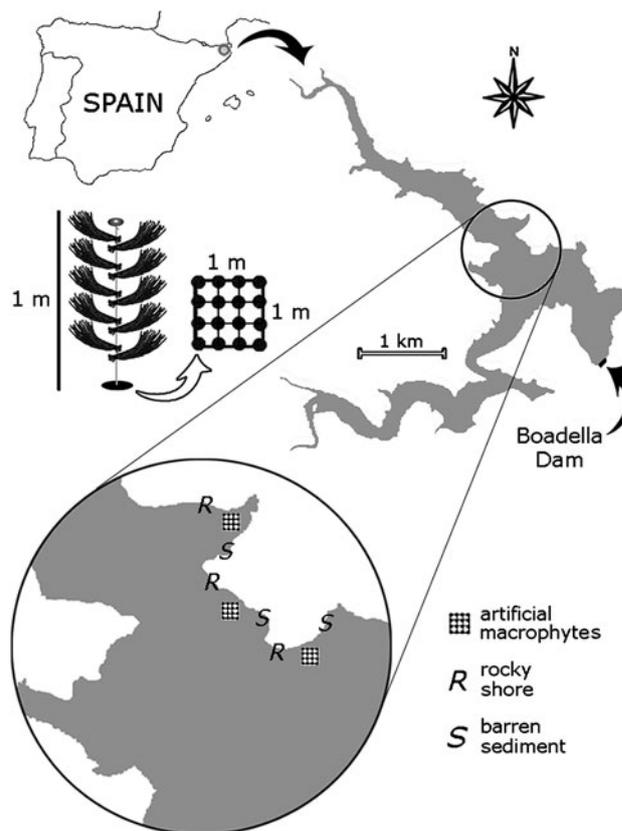


Fig. 1 Location of Boadella Reservoir (Spain), where submerged habitats were deployed. The final arrangement of the artificial habitats (replicates) and the sites where sandy beach (*S*), rocky shore (*R*) and artificial macrophytes (*hatched square*) were located are also shown

hydroelectric production and water supply (Casamitjana et al. 2003). It has a catchment area of 182 km², a maximum capacity of 62 hm³, and ca. 50 m of maximum depth. Boadella Reservoir is overall regarded as oligomesotrophic because of low nutrient concentrations of ca. 3.0 µg L⁻¹ for nitrate and <0.5 µg L⁻¹ for total phosphorus, despite having high chlorophyll *a* concentrations (>25 µg L⁻¹) and periodic cyanobacteria blooms (Serra et al. 2002; Carol et al. 2006). It is a monomictic reservoir, with high water residence time (303 days) and remarkable water level fluctuations, mainly due to dam operation regimes (Serra et al. 2002; Casamitjana et al. 2003). Drawdown in Boadella Reservoir is common in summer, when low rainfall, high evapotranspiration and high demands for electricity and water prevail (Casamitjana et al. 2003). During drawdown events, water level and reservoir volume may retract over 35 m and 75%, respectively (Serra et al. 2002), strongly affecting habitat availability and community structure. During the study period, for example, water level and reservoir volume decreased ca. 8 m and 40%, respectively (Fig. 2). Except for sparse logs and a few rocky banks, poorly complex sandy shores were the prevalent submerged habitat (LN Santos, pers. observ.). Nine

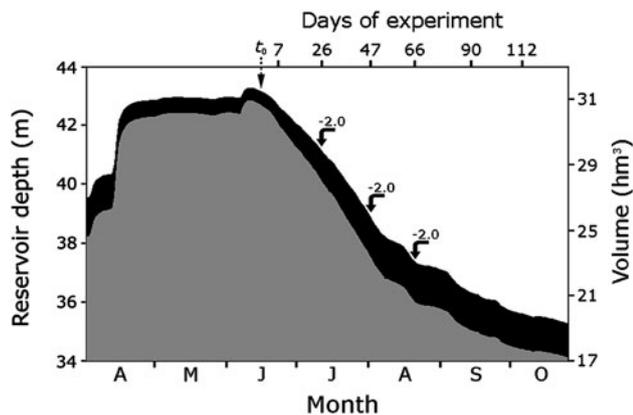


Fig. 2 Variation in water level (grey area, m a.s.l.) and volume (hm^3) in Boadella Reservoir, measured daily from 22 June to 5 October 2007. Values and arrows indicate depth and direction of artificial macrophyte relocations

introduced fishes account for most of the fish abundance and biomass in the reservoir and the chub *Squalius laietanus* is the only native fish that persists in the reservoir (Benejam et al. 2005; Carol et al. 2006).

Experimental design and visual censuses

Three types of substrates were assessed as fish habitat in Boadella Reservoir during the 2007 summer drawdown: sandy beaches (barren sediment), rocky shores, and experimentally deployed artificial macrophytes. Artificial macrophytes were similar in dimension, complexity and material to the bottom-dense structures used by Santos et al. (2008), with an architecture resembling the ribbon-like leaves of *Typha* and *Vallisneria* spp. Each macrophyte bed replicate had a 1.0 m^2 squared frame of 19-mm diameter polyvinylchloride (PVC) pipe in which four polyethylene ropes were radially attached to form nine squared-cells (Fig. 1). A 1.0 m-long polyethylene rope was then fixed at each vertex of the squared cells (16 ropes per cell), which remained vertically oriented by tying a plastic buoy to its opposite end. These ropes provided suitable substratum for tying bunches of buoyant green-brownish polypropylene ribbons (15 ribbons per bunch), measuring $40 \text{ cm} \times 1 \text{ cm} \times 1 \text{ mm}$. Ten bunches were attached to each rope, yielding $2,400 \text{ ribbons/m}^3$ for each macrophyte bed replicate. In total, three replicates of artificial macrophyte beds were experimentally deployed.

An undisturbed area located near the dam and within the lacustrine zone of the reservoir was selected to deploy the artificial macrophytes and carry out fish surveys (Fig. 1). This area was naturally depleted of aquatic vegetation and the substrate was composed mainly of sand with a variable amount of gravel. Environmental characteristics of these sites are shown in Table 1. On 15 June 2007, we deployed

Table 1 Environmental variables (mean and range) measured in the vicinity of the artificial macrophytes deployed in Boadella Reservoir from June to October 2007

Environmental variable	Mean	Range
Depth (m)	3.03	2.5–4.0
Secchi depth (m)	1.78	0.5–3.0
Temperature ($^{\circ}\text{C}$)	22.84	20.6–26.0
Oxygen (mg L^{-1})	7.48	6.4–8.6
Oxygen (% saturation)	86.94	74.3–96.3
pH	7.83	7.4–8.2
Conductivity ($\mu\text{s cm}^{-1}$)	335.60	319.0–350.0

the artificial macrophytes in the reservoir by snorkelling, tying concrete ballasts to the PVC frames in order to assure a permanent position at 3 m of depth. Concrete ballasts did not interfere with fish use because they were entirely buried in the reservoir substrate immediately after the deployment of artificial macrophytes. In addition, three replicates with similar dimensions of sandy beach (barren sediment, low-complexity) and rocky shore (2–3 rock blocks of 0.5–1.2 m diameter; intermediate-complexity) sites, located in the littoral zone (2–3 m depth), were also marked (1.0 m^2 PVC quadrates) and assigned as natural fish habitats in the reservoir (Fig. 1). A minimum distance of 50 m was set between adjacent sites to minimize the risk of fish interaction and environmental interference among treatments. The replicates of the three different treatments were spatially interspersed to assure statistical independence (Hurlbert 1984) and each replicate received a numbered floater attached to a concrete ballast to facilitate localization.

Artificial macrophytes were adjusted to reservoir water levels, which fluctuated up to 8 m during the study period (Fig. 2). Adjustments were always made after fish inspections by gently hauling the structures 2 m deeper, ensuring no structural damage of the experimental habitats and that they remained at ca. 3 m of depth during fish surveys (as in Santos et al. 2008). In the case of natural habitats, new quadrates of sandy beaches and rocky shores were selected, with equivalent dimensions and complexity of those previously monitored.

All fish associated to treatments were identified and counted by underwater census (e.g. a single snorkeller; 5–6 min/survey). Visual censuses began 7 days after the artificial macrophytes were installed (22 June 2007); all habitat treatments (natural and artificial) were surveyed approximately every 20 days until the end of summer (5 October 2007; day 112). The snorkeller inspected the habitat treatments between 9:30 and 16:30 to optimize visibility and fish identification; the order in which sites were surveyed was determined at random on each sampling occasion. Fish surveys followed the methodology proposed

by Santos et al. (2008): all fish up to 1 m from the structures were considered to be associated with habitats (natural or artificial), identified to the species level, counted, and recorded separately on an underwater writing tablet. The total length (TL) of fish was estimated visually, comparing fish size with adjacent objects of known distance (e.g. the PVC pipes were generally used for scaling, since they were available in all surveyed habitats, but polyethylene ropes and polypropylene ribbons were also used in the artificial macrophyte beds).

Data analyses

Fish richness (number of species m^{-3}), abundance (number m^{-3}) and size (mm TL) were compared among habitats and time with generalized estimating equations (GEEs), which are an extension of generalized linear models to accommodate repeated measures designs (Diggle et al. 2002). GEEs were performed with SPSS 15, using Poisson distribution and log link for richness, normal distribution and identity link for abundance (log-transformed), and gamma distribution and log link for size data.

Results

In total, 1,832 individuals of seven fish species were recorded in the natural and artificial habitats of Boadella Reservoir (Table 2). Introduced species prevailed both in richness and abundance, accounting for 91.2% of total abundance, whilst the chub *S. laietanus* was the only native species recorded, occurring in 11.1% of the fish censuses. The perch *P. fluviatilis* was by far the dominant species (65.3% of individuals). *R. rutilus*, *S. laietanus* and *Lepomis gibbosus* had intermediate abundances, although the latter species was more frequent. Fish size ranged from 10 (*L. gibbosus*) to 450 mm (*C. carpio*) of TL (Table 2).

Fish richness and abundance varied significantly among habitats and with time, but a significant habitat \times time interaction was detected only for abundance (Table 3a). Fish richness and abundance were significantly higher in artificial macrophytes than in the other two habitats (GEE contrasts: $P < 0.01$ for all; Fig. 3), and not a single fish was recorded in the low-complexity sandy shores. Fish abundance was significantly greater in rocky shores than in sandy beaches (GEE contrasts: $P < 0.01$) but richness was not (GEE contrasts: $P > 0.05$). Richness showed a unimodal variation through time, with a trend of increase until day 66 but decreasing afterwards (GEE contrasts: $P < 0.01$; Fig. 3). A similar temporal pattern was observed for fish abundance in artificial macrophytes, but no clear trend could be found for this attribute in rocky shores (Fig. 3). Fish size also varied significantly with habitat and time, with a significant habitat \times time interaction (Table 3a). Overall fish size remained quite constant (ca. 100 mm TL) in artificial macrophytes, differing from rocky shores only at the last census date (GEE contrasts: $P < 0.01$; Fig. 3).

Abundance and size of the different fish species also showed significant habitat and time variation. *P. fluviatilis*, *R. rutilus* and *A. brama* were significantly more abundant in artificial macrophytes than in the other two habitats (Table 3b), where not a single individual of these three species was recorded (Fig. 4). The abundance of these three species also varied significantly through time (Table 3b), but differed for each species (Fig. 4). *Perca fluviatilis* was the first species to colonise the artificial macrophytes, increasing progressively in number until day 66, but decreasing sharply afterwards (GEE contrasts: $P < 0.01$; Fig. 4). *Rutilus rutilus* and *A. brama* were recorded since day 26 and the first species increased numerically until day 66, leaving the artificial macrophytes after that (GEE contrasts: $P < 0.01$; Fig. 4). The size of *P. fluviatilis*, *R. rutilus* and *A. brama* also changed with

Table 2 Fish species recorded through visual censuses in the natural habitats (sandy beaches and rocky shore) and artificial macrophytes at Boadella Reservoir from June to October 2007

Fish species	Total abundance	Percentage occurrence	Total length (mm)	Origin status ^a
Cyprinidae				
<i>Abramis brama</i>	5	5.6	70–350 (223.3)	Introduced
<i>Cyprinus carpio</i>	7	9.3	350–450 (400.0)	Introduced
<i>Rutilus rutilus</i>	299	11.1	90–150 (111.0)	Introduced
<i>Squalius laietanus</i>	161	11.1	100–180 (140.0)	Native
Centrarchidae				
<i>Lepomis gibbosus</i>	157	31.5	10–100 (55.5)	Introduced
<i>Micropterus salmoides</i>	7	9.3	100–300 (191.0)	Introduced
Percidae				
<i>Perca fluviatilis</i>	1,196	31.5	50–300 (125.1)	Introduced
Total	1,832		10–450 (139.0)	

Total abundance, percentage occurrence, size range and mean (in parentheses), and native status for each species are shown

^a Relative to the Iberian Peninsula

Table 3 Habitat and temporal variations of community attributes (a), and species abundance (b) and size (c) of the fishes recorded through visual censuses at artificial macrophytes, rocky shores and sandy beaches in Boadella Reservoir from June to October 2007

Biotic variables	Habitat			Time			Habitat × time		
	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>
a) Community attributes									
Richness	17.7	1, 54	<0.01	1,174.0	4, 54	<0.01	2.0	2, 54	<0.37
Abundance	255.8	2, 54	<0.01	12,699.8	4, 54	<0.01	1.6 × 10 ⁸	4, 54	<0.01
Size	5.2	1, 25	<0.02	533.9	4, 25	<0.01	11.7	4, 25	<0.01
b) Abundance									
<i>A. brama</i>	76.2	1, 54	<0.01	89.4	2, 54	<0.01	89.4	2, 54	<0.01
<i>C. carpio</i>	11.1	2, 54	<0.01	12.0	3, 54	<0.01	12.0	3, 54	<0.01
<i>L. gibbosus</i>	173.9	2, 54	<0.01	17,584.1	4, 54	<0.01	1,686.8	4, 54	<0.01
<i>M. salmoides</i>	11.1	2, 54	<0.01	9.5	2, 54	<0.01	12.0	4, 54	<0.02
<i>P. fluviatilis</i>	192.4	1, 54	<0.01	165.6	2, 54	<0.01	165.6	2, 54	<0.01
<i>R. rutilus</i>	22.3	1, 54	<0.01	46.5	2, 54	<0.01	46.5	2, 54	<0.01
<i>S. laietanus</i>	5.0	2, 54	<0.08	129.5	3, 54	<0.01	129.5	3, 54	<0.01
c) Size									
<i>A. brama</i>	n.a.	n.a.	n.a.	1,342.7	1, 03	<0.01	n.a.	n.a.	n.a.
<i>C. carpio</i>	n.a.	n.a.	n.a.	0.0	1, 05	<1.00	n.a.	n.a.	n.a.
<i>L. gibbosus</i>	27.7	1, 17	<0.01	455,842.9	3, 17	<0.01	2.3	1, 17	<0.13
<i>M. salmoides</i>	55,022.0	1, 05	<0.01	850.3	1, 05	<0.01	850.3	1, 05	<0.01
<i>P. fluviatilis</i>	n.a.	n.a.	n.a.	6,927.8	2, 17	<0.01	n.a.	n.a.	n.a.
<i>R. rutilus</i>	n.a.	n.a.	n.a.	191.2	1, 06	<0.01	n.a.	n.a.	n.a.
<i>S. laietanus</i>	n.a.	n.a.	n.a.	381.4	1, 06	<0.01	n.a.	n.a.	n.a.

F values, degrees of freedom and significance of generalized estimating equations (GEEs) are shown

n.a. Not applicable for species that did not share two or more habitats at the same time

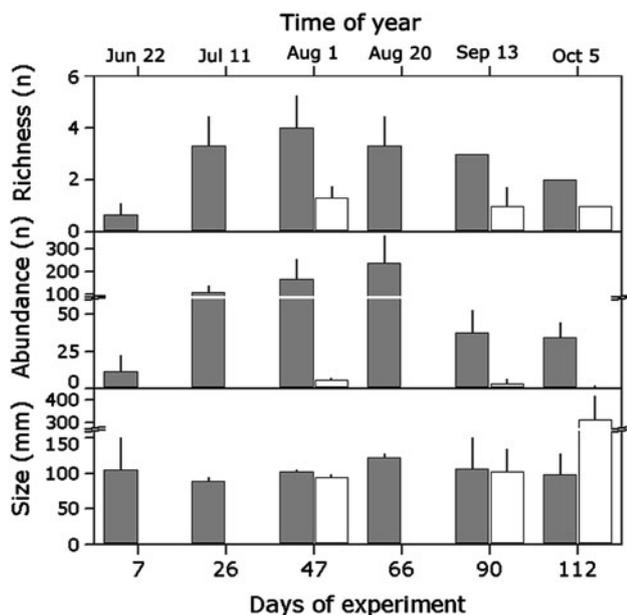


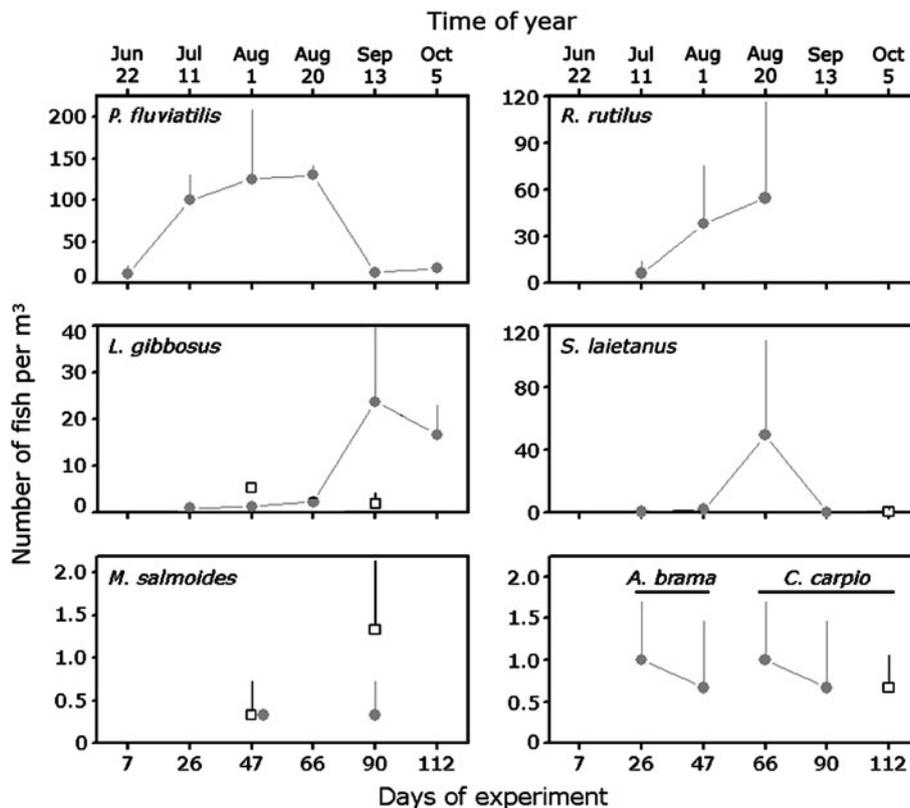
Fig. 3 Mean fish richness, abundance and size recorded by visual censuses at complex habitats (filled square artificial macrophytes; open square rocky shores). Fish richness and abundance denote, respectively, number of species and fishes per m³. Vertical lines are standard errors

time (Table 3c), with a trend of size increasing with time for the two former species and the opposite pattern for the latter (GEE contrasts; Fig. 5).

The abundance of the other four species that used both artificial macrophytes and rocky shores differed mostly among habitats. *S. laietanus* abundance showed a significant habitat × time interaction (Table 3b; Fig. 4), because it was more abundant on day 66 at artificial macrophytes and on day 112 at rocky shores, the latter coinciding with the time in which it left the artificial macrophytes. The size of *S. laietanus* showed significant temporal variation (Table 3c; Fig. 5). In the artificial macrophytes, *S. laietanus* increased progressively in size until day 90, when it averaged 150 mm of TL. After that date, only two *S. laietanus* of 180 mm TL were registered, exclusively in the rocky shores.

Lepomis gibbosus was significantly more abundant in more complex habitats (artificial macrophytes and rocky shores) than in sandy beaches (Table 3b), and it was also more abundant in artificial macrophytes than in rocky shores (GEE contrasts; Fig. 4). Abundance varied significantly with time and there was a strong habitat × time interaction (Table 3b), because *L. gibbosus* was scarce in artificial macrophytes and rocky shores until day 66 but

Fig. 4 Mean number of fish recorded by visual censuses for the seven species associated with complex habitats in Boadella Reservoir (*filled circle* artificial macrophytes; *open square* rocky shores). Vertical lines are standard errors



increased considerably in artificial macrophytes after that date (GEE contrasts; Fig. 4). The size of *L. gibbosus* varied significantly between habitats and with time, with no significant habitat \times time interaction (Table 3c). The size of *L. gibbosus* was greater in rocky shores than in artificial macrophytes, decreasing gradually with time in both habitats (GEE contrasts; Fig. 5).

The abundance of *M. salmoides* was significantly higher in more complex habitats than in sandy beaches (Table 3b), with a significant habitat \times time interaction (Table 3b; Fig. 4) because this species increased with time but only in rocky shores (GEE contrasts; Fig. 4). The size of *M. salmoides* varied significantly with habitat and time, and a significant habitat \times time interaction was detected (Table 3c). The size of *M. salmoides* was always 300 mm TL in the artificial macrophytes but remained smaller in rocky shores, with a trend of a slight increase with time in this later habitat (GEE contrasts, Fig. 5).

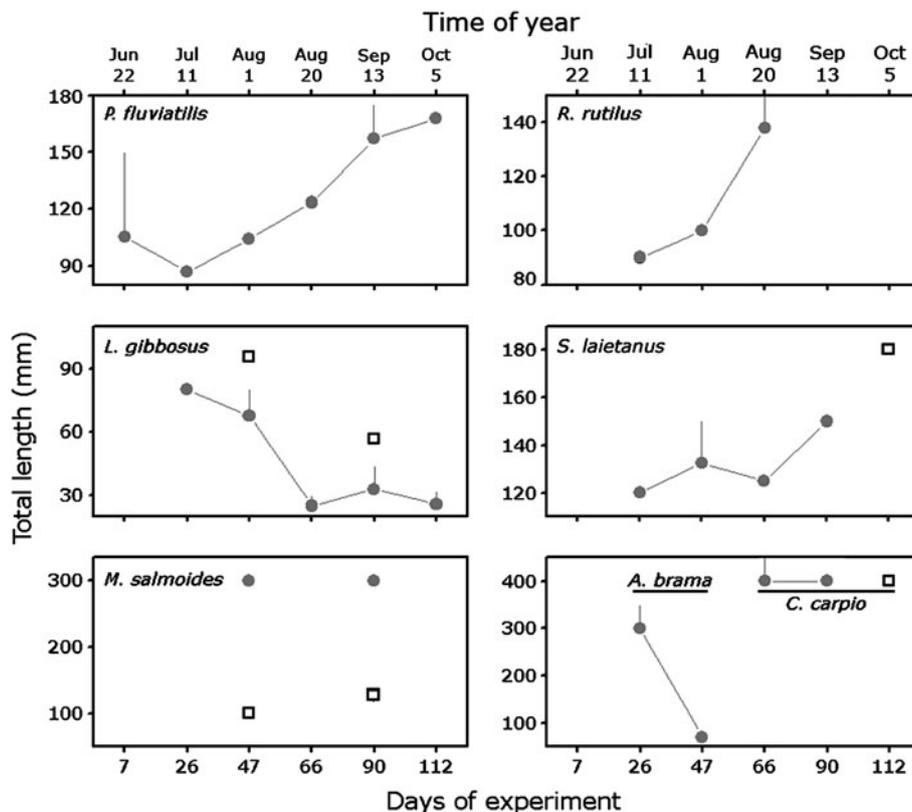
Cyprinus carpio was significantly more abundant in more complex habitats than in sandy beaches (Table 3b; GEE contrasts; Fig. 4). Its abundance varied significantly with time and a significant habitat \times time interaction also occurred because this species never shared the two habitats at the same time (Table 3b; Fig. 4). *C. carpio* was a rare species and its size did not significantly differ with habitat or time (Table 3c; Fig. 5).

Discussion

Potential of artificial macrophytes in holding fish

Fishes preferentially selected artificial macrophytes over the other two habitats (rocky shore and sandy beaches) naturally available in Boadella Reservoir, as revealed by differences on richness and abundance. Artificial macrophytes were more physically complex than the other two natural habitats and, since the experiments were performed during summer (i.e. after the reproductive season of spring), artificial macrophytes were primarily colonized by small or juvenile fish averaging 100 mm TL on size. The overall ability of artificial structures mimicking aquatic macrophytes in holding small fish was, however, rather variable. Artificial macrophytes with high physical complexity (i.e. $>1,000$ polypropylene ribbons per m^2) are generally more effective in yielding small fish than other less naturally or artificially complex habitats (Hayse and Wissing 1996; Santos et al. 2008). Conversely, few or no differences for fish abundance were found between artificial macrophytes and structure-less areas (controls) when fish size increases (>50 mm TL, Hayse and Wissing 1996; >100 mm TL, Santos et al. 2008) or when the complexity of artificial macrophytes is low (i.e. <250 polypropylene ribbons per m^2) (Jenkins and Forsythe 1984; Rold et al. 1996). Fish preference for artificial macrophytes in

Fig. 5 Mean fish size recorded by visual censuses for the seven species associated with complex habitats in Boadella Reservoir (filled circle artificial macrophytes; open square rocky shores) in Boadella Reservoir. Vertical lines are standard errors



Boadella Reservoir (i.e. 2,400 ribbons/m²) was thus probably related to two reciprocally interconnected factors: the higher complexity of artificial macrophytes relative to the other habitats and the prevalence of small fishes (≤ 100 mm TL) in the littoral zone during the study period. Physically complex habitats within the shallow littoral zone of temperate lakes are known to provide better refuge and feeding opportunities for small fishes than other structure-less or pelagic habitats (Sass et al. 2006; De Mello et al. 2009; Schou et al. 2009). Despite being recognized as one of the most effective methods to survey structurally complex habitats (Seaman and Sprague 1991), it also is possible that visual censuses may have contributed at some level to the prevalence of small fishes in the artificial macrophytes in Boadella Reservoir. Although not observed in this study, Graham (1992) and Hayse and Wissing (1996) previously reported that fish >150 mm TL often moved further way from artificial structures as divers came closer (i.e. fright response), indicating that further research is necessary to elucidate the importance of that factor on fish use analysis of submerged habitats.

Species-specific use of submerged habitats

Perca fluviatilis was the first and also the most abundant fish to be recorded during the visual censuses, but, except for the artificial macrophytes, it was not found in the other two

habitats in Boadella Reservoir. *P. fluviatilis* uses both littoral and limnetic zones, undergoing several habitat and diet shifts during its ontogeny (Byström and García-Berthou 1999). Soon after hatching in spring, *P. fluviatilis* larvae migrate from littoral to limnetic zones to feed on zooplankton until they become juveniles (10–30 mm TL) and then return to inhabit littoral vegetated areas, switching from a zooplanktivorous to a more benthivorous diet (Byström et al. 1998). *P. fluviatilis* feed on littoral macroinvertebrates until they become large enough (>150 mm TL) to prey preferentially on fish and use both littoral and limnetic zones (Eklöv 1997). Most *P. fluviatilis* recorded at Boadella Reservoir ($\sim 95\%$ of total perch abundance) were smaller than 120 mm TL and used primarily the interstices of artificial macrophytes. At this size, *P. fluviatilis* probably were younger than 1-year-old (Byström and García-Berthou 1999) and used the artificial macrophytes to avoid predation by larger cannibalistic *P. fluviatilis* (>150 mm TL) and other piscivores (e.g. 300 mm TL *M. salmoides*), which were often recorded close to the artificial structures. This hypothesis is supported by the clear decrease of *P. fluviatilis* larger than 150 mm TL in size in the artificial macrophytes.

The two most abundant cyprinids (*R. rutilus* and *S. laietanus*) also preferred the artificial macrophytes in Boadella Reservoir, but quite differently. Abundance and size of *R. rutilus* were overall related, increasing progressively at artificial macrophytes until the day 66 when the

individuals attained an average size of 140 mm TL. While associated with artificial macrophytes, *R. rutilus* apparently exhibited a high somatic investment, which can occur whenever this species does not experience a decrease in resource level (Byström and García-Berthou 1999) and because of higher zooplankton densities, especially cladocerans, within the artificial macrophytes than in the structure-less pelagic zone, as documented by De Mello et al. (2009) and Schou et al. (2009) for Scandinavian lakes. *R. rutilus* less than 140 mm TL probably decreased its predation vulnerability by using artificial macrophytes, becoming more pelagic after this size because of reduced predation risk (Byström and García-Berthou 1999). Except for day 66, the native *S. laietanus* was low in abundance, occurring at the artificial macrophytes within 120–150 mm TL of average size. The peak of *S. laietanus* abundance was on day 66 followed by a sharp decrease after that, which may be related to a severe mortality experienced by the ~120 mm TL individuals (García-Berthou and Moreno-Amich 2000) or to a shift in habitat use (Moreno-Amich et al. 2006). Both cases have been reported for native *S. laietanus* populations in Lake Banyoles, a karstic Catalan lake. In addition to the probable recruitment failures in Boadella Reservoir (see García-Berthou and Moreno-Amich 2000), *S. laietanus* may also have shifted their habitat use with increasing size, since few individuals >140 mm TL were recorded at rocky shores but not a single one within this size range was found in the artificial macrophytes.

Lepomis gibbosus, similarly to the other species, also shifted its habitat use with size. *L. gibbosus* ≤30 mm TL were recorded exclusively at artificial macrophytes, appearing by the first time on day 66 but being especially abundant after that. These small-sized *L. gibbosus* were probably young-of-the-year individuals and their use of artificial macrophytes was probably related to habitat affinity and to a reduction in predation risk (García-Berthou and Moreno-Amich 2000; Klaar et al. 2004; Sass et al. 2006). In contrast, larger *L. gibbosus* (≥60 mm TL) showed no clear preferences between rocky shores and artificial macrophytes, but their abundances were slightly higher in the former habitat when they co-occurred in both habitats. *L. gibbosus* has prominent stout spines at the anterior portion of the dorsal fin and the littoral populations of Boadella Reservoir are more deep-bodied in shape than those of most other Catalonian reservoirs (Vila-Gispert et al. 2007). Since *L. gibbosus* are mainly invertivorous and predation risk of individuals ≥60 mm TL are expected to be low in Boadella Reservoir (Vila-Gispert et al. 2007), larger *L. gibbosus* might benefit in the relatively less-complex rocky shores from increased prey capture success (Godinho et al. 1997) and from habitat more suitable for nest construction (Pérez-Bote et al. 2001).

The overall low abundances of the other fish species precluded more detailed analyses of their habitat preferences, and little information could be retrieved. As mentioned above, the presence of *M. salmoides* 300 mm TL in artificial macrophytes was apparently more related to the ability of these habitats in attracting and concentrating potential prey. Sass et al. (2006) also demonstrated that predation of 50–90 mm TL *Lepomis macrochirus*, *L. gibbosus*, *Perca flavescens* and *Pimephales promelas* by large *Micropterus* spp. and esocids peaked at the refuge edge (e.g. the boundary among physically complex and structure-less habitats) of three North American lakes. Few individuals of *C. carpio*, all large (~400 mm TL), were recorded in both artificial macrophytes and rocky shores, but all individuals associated with artificial macrophytes were recorded sucking and masticating the polypropylene ribbons, denoting that the attached organisms could be a food resource. The importance of periphyton and macro-invertebrates for the use of artificial structures by fish (Moring et al. 1986; Santos et al. 2008) or in *C. carpio* diet (García-Berthou 2001) has been previously documented.

Implications on conservation and management

This study demonstrates that the deployment of complex structures, such as artificial macrophytes, may be a good alternative to expand habitats for small fish (<150 mm TL) in Boadella Reservoir and other similar temperate reservoirs that experience remarkable water level fluctuations. Because of non-natural water level fluctuations, which are intrinsic to reservoir operation routines, the growth of aquatic vegetation is impaired and other physical structures, such as logs and rocks, become largely unavailable to aquatic organisms (Agostinho et al. 2007). Acute water level fluctuations can pose several threats to fish survival, leading to less diversified fish assemblages that are more susceptible to ecological impacts (Piet 1998; Rahel 2002). Therefore, artificial macrophytes, in adequate amounts and complexity, could increase fish survival in these reservoirs through many non-mutually exclusive ways, such as providing substrata for spawning (Nash et al. 1999; Sandström and Karås 2002), creating refuge against predation (Hayse and Wissing 1996; Santos et al. 2008) or enhancing food availability (Winfield 1986). Spawning requirements were not addressed in the present study, but we hypothesise that both predation risk and food restriction, which were the major attributes harshened by the drawdown, were the main driving forces of fish use of artificial macrophytes in Boadella Reservoir.

In addition, there are other issues arising from this work that must be taken into account by further studies or large-scale habitat enhancement programmes based on artificial structures. First, artificial structures must be conceived to

be functionally effective in various water level scenarios, implying the need for artificial structures that are more self-adjustable to variation in water level. Santos et al. (2008) tested mid-water structures, less sensitive to water level fluctuations, that could be a potential alternative, but further research is necessary since water levels fluctuated only ~5.0 m in that study. Mid-water structures mimicking free-floating macrophytes can also be more effective in holding temperate fish than benthic structures simulating submerged plants (Meerhoff et al. 2007). Further studies on the resistance of the material applied in artificial structures are, however, critical since, in contrast to artificial reefs deployed in marine systems, artificial structures placed in freshwater tend to decay physically and lose effectiveness with time (Seaman and Sprague 1991). The potential of synthetic macrophytes for adverse environmental effects should also be carefully assessed, since artificial structures, in addition to overfishing and decreases on fish growth, may release pollutants to the water (i.e. leachates from scrap tires), and become unaesthetic or a navigation hazard, especially in reservoirs where severe drawdown and water level fluctuation occur frequently (Bolding et al. 2004).

The potential of artificial structures for benefiting either indigenous or non-native species must be addressed prior to any ecosystem intervention. Even though artificial macrophytes have played an important role for juveniles of the Mediterranean endemic *S. laietanus*, we do not expect much ecological benefit for this species by just adding artificial structures to Catalan reservoirs, which are generally dominated in abundance by invasive species (Carol et al. 2006). Two non-mutually exclusive alternatives can be used to solve this dilemma: (1) identify those artificial structures that give advantage to *S. laietanus* and other native species over other introduced species; and (2) manage those artificial structures with higher ability in attract or concentrate fish to intensify the harvest of invasive species. Despite the virtual unawareness on the use of artificial structures that are able to affect a single species in particular, studies on angling at artificial attractors have provided other perspectives on the use of artificial structures for invasive species removal (Wilbur 1978; Johnson and Lynch 1992; Rogers and Bergersen 1999; Bolding et al. 2004). Finally, the present study showed that artificial structures mimicking aquatic macrophytes, apart from their potential to mitigate the drawdown impacts on reservoir fish assemblages, can be also applied to investigate fish responses to environmental disturbances and as assisting tools in other ecosystem experiments, due to their ability in attract and concentrate fish.

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References

- Agostinho AA, Thomaz SM, Miranda LE, Bini LM, Gomes LC, Suzuki HI (1999) Patterns of colonization in neotropical reservoirs, and prognoses on aging. In: Tundisi JG, Straskraba M (eds) Theoretical reservoir ecology and its applications. International Institute of Ecology/Backhuys Publishers/Brazilian Academy of Sciences, Rio de Janeiro, pp 227–265
- Agostinho AA, Gomes LC, Pelicice FM (2007) Ecologia e Manejo dos Recursos Pesqueiros em Reservatórios do Brasil. EDUEM, Maringá, p 501
- Beklioglu M, Altinayar G, Tan CO (2006) Water level control over submerged macrophyte development in five shallow lakes of Mediterranean Turkey. Arch Hydrobiol 166:535–556
- Benejam L, Carol J, Alcaraz C, García-Berthou E (2005) First record of the common bream (*Abramis brama*) introduced to the Iberian Peninsula. Limnetica 24:273–274
- Benejam L, Benito J, Ordóñez J, Armengol J, García-Berthou E (2008) Short-term effects of a partial drawdown on fish condition in a eutrophic reservoir. Water Air Soil Pollut 190:3–11
- Benoît J, Legault M (2002) Assessment of the feasibility of preventing reproduction of lake charr, *Salvelinus namaycush*, in shallow areas of reservoirs affected by drawdowns. Environ Biol Fish 64:303–311
- Bolding B, Bonar S, Divens M (2004) Use of artificial structure to enhance angler benefits in lakes, ponds, and reservoirs: a literature review. Rev Fish Sci 12:75–96
- Byström P, García-Berthou E (1999) Density dependent growth and size specific competitive interactions in young fish. Oikos 86:217–232
- Byström P, Persson L, Wahlström E (1998) Competing predators and prey-juvenile bottlenecks in whole-lake experiments. Ecology 79:2153–2167
- Carol J, Benejam L, Alcaraz C, Vila-Gispert A, Zamora L, Navarro E, Armengol J, García-Berthou E (2006) The effects of limnological features on fish assemblages of 14 Spanish reservoirs. Ecol Freshw Fish 15:66–77
- Casamitjana X, Serra T, Colomer J, Baserba C, Pérez-Losada J (2003) Effects of the water withdrawal in the stratification patterns of a reservoir. Hydrobiologia 504:21–28
- De Mello FT, Meerhoff M, Pekcan-Hekim Z, Jeppesen E (2009) Substantial differences in littoral fish community structure and dynamics in subtropical and temperate shallow lakes. Freshw Biol 54:1202–1215
- Diggle PJ, Heagerty P, Liang KY, Zeger SL (2002) The analysis of longitudinal data. Oxford University Press, Oxford, p 379
- Dudgeon D, Arthington AH, Gessner MO, Kawabata ZI, Knowler DJ, Leveque C, Naiman RJ, Prieur-Richard AH, Soto D, Stiassny MLJ, Sullivan CA (2006) Freshwater biodiversity: importance, threats, status and conservation challenges. Biol Rev 81:163–182
- Eklöv P (1997) Effects of habitat complexity and prey abundance on the spatial and temporal distributions of perch (*Perca fluviatilis*) and pike (*Esox lucius*). Can J Fish Aquat Sci 54:1520–1531
- Engel S (1995) Eurasian watermilfoil as a fishery management tool. Fisheries 20:20–27
- García-Berthou E (2001) Size- and depth-dependent variation in habitat and diet of the common carp (*Cyprinus carpio*). Aquat Sci 63:466–476

- García-Berthou E, Moreno-Amich R (2000) Introduction of exotic fish into a Mediterranean lake over a 90-year period. *Arch Hydrobiol* 149:271–284
- Godinho FN, Ferreira MT, Cortes RV (1997) The environmental basis of diet variation in pumpkinseed sunfish, *Lepomis gibbosus*, and largemouth bass, *Micropterus salmoides*, along an Iberian river basin. *Environ Biol Fish* 50:105–115
- Graham RJ (1992) Visually estimating fish density at artificial structures in Lake Anna, Virginia. *North Am J Fish Manage* 12:204–212
- Hayse JW, Wissing TE (1996) Effects of stem density of artificial vegetation on abundance and growth of age-0 bluegills and predation by largemouth bass. *Trans Am Fish Soc* 125:422–433
- Hurlbert SH (1984) Pseudoreplication and the design of ecological field experiments. *Ecol Monogr* 54:187–211
- Jenkins GD, Forsythe TD (1984) An evaluation of Berkley's Fish-Hab fish attractors in a lowland impoundment. TVA land between the lakes. Fisheries Management Section, Kentucky
- Johnson DL, Lynch WL (1992) Panfish use of and angler success at evergreen tree, brush, and stake-bed structures. *North Am J Fish Manage* 12:222–229
- Klaar M, Copp GH, Horsfield R (2004) Autumnal habitat use of non-native pumpkinseed *Lepomis gibbosus* and associations with native fish species in small English streams. *Folia Zool* 53:189–202
- Meerhoff M, Iglesias C, de Mello FT, Clemente JM, Jensen E, Lauridsen TL, Jeppesen E (2007) Effects of habitat complexity on community structure and predator avoidance behaviour of littoral zooplankton in temperate versus subtropical shallow lakes. *Freshw Biol* 52:1009–1021
- Miranda LE (1996) Development of reservoir fisheries management paradigms in the twentieth century. In: Miranda LE, DeVries DR (eds) Multidimensional approaches to reservoir fisheries management, 16th American Fisheries Society Symposium, Bethesda, pp 3–16
- Moreno-Amich R, Pou-Rovira Q, Vila-Gispert A, Zamora L, García-Berthou E (2006) Fish ecology in Lake Banyoles (NE Spain): a tribute to Ramon Margalef. *Limnetica* 25:321–334
- Moring JR, Eiler PD, Negus MT, Gibbs KE (1986) Ecological importance of submerged pulpwood logs in a Maine reservoir. *Trans Am Fish Soc* 115:335–342
- Nash KT, Hendry K, Cragg-Hine D (1999) The use of brushwood bundles as fish spawning media. *Fish Manage Ecol* 6:349–355
- Pérez-Bote JL, Soringuer MC, Rodríguez-Jiménez AJ (2001) Nest characteristics and nesting sites of the pumpkinseed sunfish *Lepomis gibbosus* (L., 1758) (Osteychthyes, Centrarchidae) in the mid-Guadiana river basin: river versus reservoir. *Zool Baetica* 12:3–13
- Piet GJ (1998) Impact of environmental perturbation on a tropical fish community. *Can J Fish Aquat Sci* 55:1842–1853
- Rahel FJ (2002) Homogenization of freshwater faunas. *Annu Rev Ecol Syst* 33:291–315
- Rogers KB, Bergersen EP (1999) Utility of synthetic structures for concentrating adult northern pike and largemouth bass. *North Am J Fish Manage* 19:1054–1065
- Rold RE, McComish TS, van Meter DE (1996) A comparison of cedar trees and fabricated polypropylene modules of fish attractors in a strip mine impoundment. *North Am J Fish Manage* 16:223–227
- Sammons SM, Dorsey LG, Bettolli PW, Fiss FC (1999) Effects of reservoir hydrology on reproduction by largemouth bass and spotted bass in Normandy reservoir, Tennessee. *North Am J Fish Manage* 19:78–88
- Sandström A, Karås P (2002) Tests of artificial substrata as nursery habitat for young fish. *J Appl Ichthyol* 18:102–105
- Santos AFGN, Santos LN, Araújo FG (2004) Water level influences on body condition of *Geophagus brasiliensis* (Perciformes, Cichlidae) in a Brazilian oligotrophic reservoir. *Neotrop Ichthyol* 2:151–156
- Santos LN, Araújo FG, Brotto DS (2008) Artificial structures as tools for fish habitat rehabilitation in a neotropical reservoir. *Aquat Conserv Marine Freshw Ecosyst* 18:896–908
- Sass GG, Gille CM, Hinke JT, Kitchell JF (2006) Whole-lake influences of littoral structural complexity and prey body morphology on fish predator–prey interactions. *Ecol Freshw Fish* 15:301–308
- Schou MO, Risholt C, Lauridsen TL, Søndergaard M, Grønkjær P, Jacobsen L, Berg S, Skov C, Brucet S, Jeppesen E (2009) Restoring lakes by using artificial plant beds: habitat selection of zooplankton in a clear and a turbid shallow lake. *Freshw Biol* 54:1520–1531
- Seaman W, Sprague L (1991) Artificial habitats for marine and freshwater fisheries. Academic Press, San Diego, p 284
- Serra T, Colomer J, Baserba C, Soler M, Casamitjana X (2002) Quantified distribution of diatoms during the stratified period of Boadella reservoir. *Hydrobiologia* 489:235–244
- Smiley PC, Dibble ED (2006) Evaluating the feasibility of planting aquatic plants in shallow lakes in the Mississippi Delta. *J Aquat Plant Manage* 44:73–80
- Strakosh TR, Eitzmann JL, Gido KB, Guy CS (2005) The response of water willow *Justicia americana* to different water inundation and desiccation regimes. *North Am J Fish Manage* 25:1476–1485
- Strange RJ, Kittrell WB, Broadbent TD (1982) Effects of seeding reservoir fluctuation zones on young-of-the-year black bass and associated species. *North Am J Fish Manage* 4:307–315
- Summerfelt RC (1993) Lake and reservoir habitat management. In: Kohler CC, Hubert WA (eds) Inland fisheries management in North America. American Fisheries Society, Bethesda, pp 231–261
- Sutela T, Mutenia A, Salonen E (2002) Relationship between annual variation in reservoir conditions and year-class strength of peled (*Coregonus peled*) and whitefish (*C. lavaretus*). *Hydrobiologia* 485:213–221
- Vila-Gispert A, Fox MG, Zamora L, Moreno-Amich R (2007) Morphological variation in pumpkinseed *Lepomis gibbosus* introduced into Iberian lakes and reservoirs; adaptations to habitat type and diet? *J Fish Biol* 71:163–181
- Wilbur RL (1978) Two types of fish attractors compared in Lake Tohopekaliga, Florida. *Trans Am Fish Soc* 107:689–695
- Wills TC, Bremigan MT, Hayes DB (2004) Variable effects of habitat enhancement structures across species and habitats in Michigan reservoirs. *Trans Am Fish Soc* 133:399–411
- Winfield IJ (1986) The influence of simulated aquatic macrophytes on the zooplankton consumption rate of juvenile roach (*Rutilus rutilus*), rudd (*Scardinius erythrophthalmus*) and perch (*Perca fluviatilis*). *J Fish Biol* 29:37–48
- Yamamoto T, Kohmatsu Y, Yuma M (2006) Effects of summer drawdown on cyprinid fish larvae in Lake Biwa, Japan. *Limnology* 7:75–82